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1.—The Clinidae of Western Australia (Teleostei, Blennioidea)

by N. E. Milward*

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Abstract

A taxonomic review of the Western Australian fishes of the family Clinidae is given, together with notes on their distribution and biology. Keys to the genera, *Cristiceps* with two species and *Petraites* with five species, are included.

Introduction

The origin of the family Clinidae appears to have been in the seas of the New World (Hubbs 1952), with dispersal of representatives to the Australian region via South America and South Africa. The number of Australian species is small, mainly cool to temperate water forms. From Western Australia seven species are known, two of the genus *Cristiceps* Cuvier and Valenciennes, 1836, and five of *Petraites* Ogilby, 1885.

The papers of McCulloch (1908), Scott (1939, 1955), and Whitley (1945) provide taxonomic reviews and keys to some of the Australian species but there is virtually nothing in the literature on their biology. The purpose of this contribution is to review the Western Australian clinids, giving fuller descriptions of the species, information on their distribution, and notes on their biology.

This paper is based on part of studies of blennioid fishes carried out over a wide range of the Western Australian coastline, from the Monte Bello Islands (lat. 20° 30' S., long. 115° 25' E.) to Denmark (lat. 35° 0' S., long. 117° 5' E.). Extensive collections were made in the littoral and sub-littoral by poisoning, hand-netting, and trapping, but compared with other blennioids, e.g. blenniids and tripterygiids, the number of clinids taken was relatively few. Other specimens examined were a few received from Mr. R. J. McKay of the Fisheries Department (now of the Western Australian Museum), Dr. A. R. Main of the Zoology Department, University of Western Australia, and Dr. G. M. Storr of the Western Australian Museum, and those in the Western Australian Museum Collection, which was kindly made available for study by the Director, Dr. W. D. L. Ride.

Except for a few specimens placed in the Australian Museum, Sydney, almost all the material has been added to the collection at

the Western Australian Museum. In the listing of material examined collection localities and dates are given, together with catalogue numbers for specimens lodged either at the Western Australian Museum, without prefix or preceded by the letter P, or at the Australian Museum, preceded by the letters IB.

I wish to thank Dr. H. Waring, Professor of Zoology, University of Western Australia, in whose department the work was carried out as partial fulfillment for M.Sc. degree, and Dr. E. P. Hodgkin and Dr. A. R. Main for assistance during the study. The work was supported by a Research Grant from the University of Western Australia.

Australian Clinidae

All the Australian species belong to the sub-family Clininae as defined by Hubbs (1952).

They may be distinguished as blennioid fishes having moderately to very elongate, often laterally compressed, bodies; small and frequently inconspicuous cycloid scales; conical jaw teeth; gill-membranes united, free from isthmus; a small hook-like process on inner margin of pectoral girdle beneath the operculum; long dorsal fin of many spines and a few rays, the anterior spines often as a distinct crest which may or may not be connected to the following spine by membrane; pelvic fins jugular, of a spine, generally concealed, and two to four rays; all fin rays simple; and cirri generally present over anterior nares and orbits.

Previously the Clinidae has not been clearly delineated in the Australian literature. In check-lists McCulloch (1929) and Whitley (1948) have variously included within the family species referable to the Tripterygiidae. Marshall (1964) on Queensland fishes places under the name Clininae the tripterygiid species, while at the same time including the true clinids in the Blenniidae. The above diagnosis clearly excludes species of the Tripterygiidae and distinguishes clinids from the Blenniidae.

Three genera are represented in Australian waters: *Clinus* Cuvier, 1816, *Cristiceps* Cuvier and Valenciennes, 1836, and *Petraites* Ogilby,

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1885. The genera *Heteroclinus* Castelnau, 1872, and *Neoblennius* Castelnau, 1875, have no validity (Waite 1923).

Lack of obvious, clear-cut morphological differences between *Clinus*, *Cristiceps*, and *Petraites* has caused taxonomic difficulties (McCulloch 1908; Scott 1955). The species of the three genera intergrade in many characters, *Petraites* being erected by Ogilby (1885), on a suggestion by Macleay (1882), to receive "those homeless fishes, which oscillate between the other two genera". The main character employed to separate the genera has been the degree of attachment by membrane of the third to the fourth dorsal fin spine. This in itself is a variable character but when taken in combination with other characters, namely the form of the supraorbital tentacles, numbers of dorsal fin spines and dorsal and pectoral fin rays, position of the first dorsal spine in relation to the eye, and the degree of membranous attachment of the last dorsal fin ray to the caudal peduncle, three distinct, seemingly natural, groups emerge and McCulloch's (1908) recommendation that the three genera should be retained is supported.

Key to Australian genera of Clinidae

1. First dorsal spine over or just in front of eye; membrane from last dorsal ray not extending to caudal fin; supra-orbital tentacles long, with narrow base *Cristiceps*
 First dorsal spine behind eye; membrane from last dorsal ray extending to caudal fin; supra-orbital tentacles short and rounded, or, if long, with broad base 2
2. (1) Third dorsal spine connected by membrane only to basal portion of fourth; 2nd dorsal fin with 31 or less spines *Petraites*
 Third dorsal spine connected by membrane to middle or upper half of fourth; 2nd dorsal fin with 32 or more spines *Clinus*

In Western Australian waters two genera are represented: *Cristiceps* with two species and *Petraites* with five species. The listing of *Clinus perspicillatus* Cuvier and Valenciennes, 1936, by Whitley (1948) appears to have resulted from a mis-identified specimen of *Petraites antinectes* (Günther) in the Western Australian Museum collection and with this deletion *Clinus* remains unrecorded from this State.

Genus *Cristiceps* Cuvier and Valenciennes, 1836
Cristiceps Cuvier and Valenciennes, 1836, Hist. Nat. Poiss., xi, p.402—type by original designation
Cristiceps australis Cuv. and Val.

Key to Western Australian species of *Cristiceps*

- Inner ray of ventral fin much less than half length of middle ray; dorsal rays equally spaced *australis*
 Inner ray of ventral fin at least half length of middle ray; last two dorsal rays widely spaced from those preceding *aurantiacus*

Cristiceps australis Cuvier and Valenciennes, 1836

Cristiceps australis Cuvier and Valenciennes, 1836, Hist. Nat. Poiss., xi, p.402.

Cristiceps axillaris Richardson, 1846, in Discoveries in Australia (Stokes), 1, p.486.
Christiceps splendens (sic) Castelnau, 1872, Proc. Zool. Acclim. Soc. Vict., 1, p.244.
Cristiceps howittii Castelnau, 1873, ibid., 2, p.48.
Cristiceps macleayi Castelnau, 1879, Proc. Linn. Soc. N.S.W., 3, p.385.
Cristiceps pallidus Macleay, 1882, Proc. Linn. Soc. N.S.W., 6, p.26.

Material examined. 22 specimens, varying in total length from 63 to 216 mm. Lancelin I. 7.iv.58; Cottesloe 10.vi.24 P879, 11.vii.27 P946; Rottnest I. 31.iii.56 P6182, 17.ix.56 P6185; Fremantle, offshore 3.ix.54 P3738; Garden I., offshore -vii.57; Coogee, south of Fremantle 26.vii.26 P921; Rockingham 4.v.18 P606; Peel Inlet 19.iv.44 P2611; Cape Bouvard, offshore 18.x.56 IB5161-3; Busselton 4.iv.38 P1867, 27.ii.53; Albany 27.iv.11 11279-80, -iv.11 12892-3, 6.viii.35 P1470, 30.ix.41 P2319, 26.iv.44 P2614.

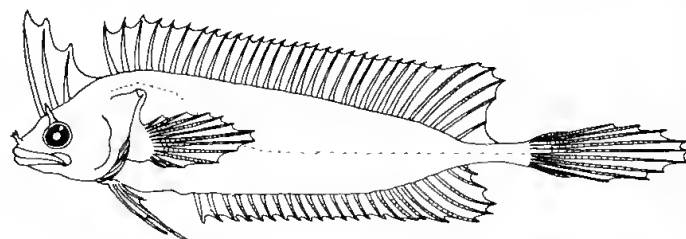


Figure 1.—*Cristiceps australis* Cuv. & Val., P6185, male, 94 mm, Rottnest I., 17.ix.56.

Description. Body moderately elongate, laterally compressed. Eyes large. Snout pointed. Lips reach almost to posterior margin of eye. Nasal tentacle a tubular pedicel palmately bearing a few short filaments. Supra-orbital tentacle long and slender, either simple with entire border or notched on inner and/or outer edge. High dorsal crest originating over eye, 1st and 2nd spines about equal in height, 3rd slightly more than half height of first two; each crest spine with soft extension which supports membrane above hard filaments. Membrane from 3rd spine generally just short of but may be joined to base of 4th spine. Margin of long dorsal fin fairly uniformly straight; soft extensions at the end of spines accentuate incisions in membrane between filaments; rays usually equally spaced, posterior ones shorter so that fin ends squarely; last ray completely united to about half-way along caudal peduncle by membrane. Anal fin spines about equal to anterior rays; rays increase in length posteriorly, 4th last the longest, final three decreasing in size making fin angularly pointed at end; base only of last ray joined to caudal peduncle. Pectoral fin extending beyond origin of anal fin in small specimens but short of it in large ones. Two outer rays of ventral fin long and free for most of their length, inner one short and much less than half length of middle ray. Caudal fin lanceolate, with stout inner rays and a short, slender one above and below. Lateral line a series of short tubes, arching over pectoral fin and continuing along mid-side to tail.

Colour in life. Very variable, bright green to brown and red. Marked with darker bands and silvery spots.

Colour in formalin. Body, head, and fins fairly uniform yellow-orange.

Fin counts. The numbers of spines and rays in the fins of the 22 specimens examined were D. iii, xxvi-xxviii, 5-8; A. ii, 22-26; P. 11; V. (i), 3; C. 9+2. (Counts from individual specimens of this and the other species are given in unpublished thesis, Milward (1962). Note: the spine in the ventral fin is reduced and concealed; the caudal fin is composed of nine fairly stout, inner rays and two weak, outer rays.)

The counts recorded, with only one exception, lie within the overall ranges given by McCulloch (1908) for 21 specimens from New South Wales, Victoria, and Western Australia, D. iii, xxvi-xxix, 6-8; A. ii, 24-26; V. 3; and for 7 specimens from New South Wales, South Australia, and Western Australia, D. iii, xxvi-xxviii, 6-7; A. ii,

22-24; V. 3. The single transgression, the count of 5 rays in the dorsal fin, was found in a specimen of 97 mm collected at Rottnest Island. Only one of the specimens examined had an anal fin ray count of 26, the remainder having 22-24 in agreement with the lower range given by McCulloch. Similarly, only one, the same specimen of 159 mm collected at Albany, had 8 rays, i.e. the upper limit, in the dorsal fin.

From McCulloch's paper it may be noted that his Western Australian specimens with the higher counts came from King George Sound (Albany), whereas those with the lower counts came from Fremantle. If the counts made in the present study are separated into those derived from specimens collected at Albany and those from specimens taken at other localities, differences between the two groups are also evident (see Table 1).

TABLE 1

Fin counts in Western Australian specimens of <i>C. australis</i>													
2nd dorsal fin spines				2nd dorsal fin rays				Anal fin rays					
Specimens from:	26	27	28	5	6	7	8	22	23	24	25	26	
Busselton and northwards	1	11	3	1	12	2	—	5	5	3	—	—	
Albany	—	1	5	—	2	4	1	—	1	4	—	1	

Comparisons by Student's *t* tests show that for each of the characters having variation (numbers of 2nd dorsal fin spines, 2nd dorsal fin rays, and anal fin rays) the differences are significant at the 1% level between counts for the two groups of specimens. The lower counts from the northern localities suggest the possible influence of higher temperatures during development (see Hubbs 1922, and Taning 1950, 1952) but both McCulloch's counts and the lack of differences between samples from the localities north of Busselton tend to negate this explanation. No other reasons can validly be suggested from the few specimens available and the observations made, so the underlying causes for the differences between the Albany and other specimens must for the present remain unexplained.

Distribution. Australia: Western Australia, South Australia, Tasmania, Victoria, New South Wales (McCulloch 1929), Queensland (specimens collected Moreton Bay, Dec. 1962—author), Lord Howe Island (Waite 1900). Northern coast of North Island, New Zealand (Hutton 1873).

Cristiceps aurantiacus Castelnau, 1879

Cristiceps aurantiacus Castelnau, 1879, Proc. Linn. Soc. N.S.W., 3, p.386.

Cristiceps pictus Macleay, 1882, Proc. Linn. Soc. N.S.W., 6, p.25.

Material examined. 11 specimens, varying in total length from 45 to 244 mm. West Wallaby I., Houtman's Abrolhos 20.iv.29; Geraldton -x.09 10186, 25.iv.57 IB5165; Lancelin I., off-shore 23.i.58 P6180-1; Fremantle 21.iv.22 P801; Straggler's Reef, off Fremantle 24.v.59 P4447; Point Peron 11.ix.33 P1309, 26.x.36 P1706; Harvey Beach -vi.57 P6291; Unlocalised -iv.12.

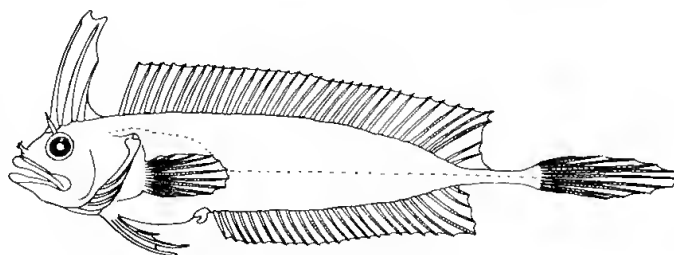


Figure 2.—*Cristiceps aurantiacus* Castelnau. P6181, male, 94 mm, Lancelin I., 23.i.58.

Description. Body moderately elongate, laterally compressed. Eyes large. Snout pointed. Lips reach to or slightly beyond posterior margin of eye. Nasal tentacle a tubular pedicel bearing a few simple filaments. Supra-orbital tentacle long and slender, tapering to a point, either simple with entire border or notched on inner or both edges. High dorsal crest originating just before or over anterior part of eye and enveloped in a thick, flabby membrane. Membrane from 3rd dorsal spine does not reach base of 4th. Margin of long dorsal fin fairly uniformly straight, cut square posteriorly; last two rays widely spaced from those preceding, with transparent membrane between; last ray entirely united to about half-way along caudal peduncle by membrane. Anal fin spines slightly shorter than 1st ray; rays increase in length posteriorly, 4th last the longest, final three decreasing in size making fin angularly pointed at end; last ray only basally connected to peduncle by membrane. Pectoral fin extending to just beyond origin of anal fin or some distance short of it. Ventral fin of a concealed spine and three rays, outer two longest, inner at least half length of middle one; rays broadly

webbed by thick membrane. Caudal fin lanceolate, with stout inner rays and a short, slender one above and below. Lateral line a series of tubes commencing over operculum, extending a short distance almost horizontally and then dropping obliquely to mid-line, whence it continues to tail.

Colour in life. Not handled alive. Marshall (1964) gives the following description: "Colour a beautiful clear orange-yellow, with the fins yellow; there are 4 almost vertical hyaline patches on the second dorsal, the first about the seventh and eighth spines, another about the thirteenth and fourteenth, another about the twentieth and twenty-first and the last on the two last short rays. Some examples are reddish with the fins dark purple, with minute blackish dots and pectorals and ventral fins barred with yellow."

Colour in formalin. Body, head, and fins a fairly uniform whitish to yellow-orange colour. A darker orange streak passing through eye and over cheek, just behind angle of lip, in some specimens.

Colour in alcohol. A specimen initially preserved in methylated spirits profusely spotted with brown dots over entire head, body, and fins against a yellow background. Brown streak present from supra-orbital tentacle through eye and down cheek.

Fin counts. The numbers of spines and rays in the fins of the 11 specimens examined were D. iii, xxix-xxxi, 4-5+2; A. ii, 23-25; P. 11; V. (i), 3; C. 9+2.

These counts agree closely with those given by McCulloch (1908) with the exception of the thirty-one rays in the 2nd dorsal fin, which is higher than hitherto recorded. This higher count was found in 3 specimens of 45 mm from offshore, Lancelin Island, 180 mm from Straggler's Reef, off Fremantle, and 244 mm from Point Peron.

Distribution. Australia: Western Australia (Whitley 1945), New South Wales (McCulloch 1929). Lord Howe Island (Ogilby 1889). North-east coast of North Island, New Zealand (Griffin 1926).

Genus **PETRAITES** Ogilby, 1885

Petraites Ogilby, 1885, Proc. Linn. Soc. N.S.W. 10, p.225—type by original designation *Petraites heptacolus* Ogilby.

Key to Western Australian species of *Petraites*

1. Ventral fin with two rays; dorsal fin with two rays *nasutus*
 Ventral fin with three rays; dorsal fin with three or four rays 2
2. (1) Three rays of ventral fin approximately equal, supra-orbital tentacle with long outer filament *equiradiatus*
 Three rays of ventral fin unequal, outer two longer and stouter than inner one; supra-orbital tentacle without a long filament 3
3. (2) 1st and 2nd dorsal fin rays with a wide space between *heptacolus*
 Dorsal fin rays more or less equally spaced, 1st and 2nd not widely separated 4
4. (3) Dorsal fin with 3 + 29-31 spines and 3 (occasionally 4) rays *antinectes*
 Dorsal fin with 3 + 25-27 spines and 4 (occasionally 3) rays *roseus*

Note. The construction of a workable, yet simple, key to the *Petraites* spp. is extremely difficult. Use of body proportions, e.g. deep or slender, as employed by McCulloch (1908), has limitations due to the allometric growth of the species. Diagnosis by means of differences in fin counts is not wholly satisfactory either, because of the possibility of undiscovered variation, but from the material examined the constancy of the differences used in the above key indicates that they will be reliable for most, if not all, specimens.

***Petraites nasutus* (Gunther), 1861**

Cristiceps nasutus Gunther, 1861, Cat. Fish. Brit. Mus., iii, p.273.

Cristiceps fasciatus Macleay, 1882, Proc. Linn. Soc. N.S.W., 6, p.19.

Clinus whiteleggii Ogilby, 1894, Proc. Linn. Soc. N.S.W., (2), 9, p.371.

Petraites fasciatus; McCulloch, 1908, Rec. Aust. Mus., 7, p.42.

Petraites nasutus; Whitley, 1941, Aust. Zool., 10, p.38.

Material examined. One specimen measuring 49mm total length. Rottnest I. 21.i.54 P6763.

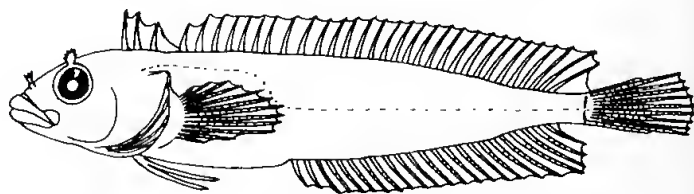


Figure 3.—*Petraites nasutus* (Gunther), P6763, female, 49 mm, Rottnest I., 21.i.54.

Description. Moderately elongate, rather slender body. Large eyes. Snout pointed. Lips not reaching posterior margin of eye. Nasal cirrus trifid, on a short tubular pedicel. Supra-orbital tentacle a broad, flat flap with irregular filaments around margin. First three dorsal spines separated as a crest but no higher than remainder of fin; 1st spine just behind vertical from pre-opercular margin; membrane from 3rd spine connected to base of 4th. Dorsal fin spines long, increasing slightly in length posteriorly so that fin border more or less horizontal; 2nd ray shorter than 1st and entirely connected to whole of caudal peduncle by membrane. Two anal spines shorter than rays, which are longest posteriorly; last ray connected to only about a third of peduncle. Pectoral fin rounded, not quite reaching origin of anal fin. Ventral fin of a concealed spine and two slender rays. Caudal fin sub-truncate. Lateral line a series of tubes commencing over operculum, running parallel to back for a short distance, but not as far as vent, then dropping obliquely to mid-line whence it continues to tail.

Colour in life. McCulloch (1908), for New South Wales specimens, states "In colour it may be anything from dark green without markings to pale green with darker bands and silvery or transparent markings. Specimens living in the pink coralline sea-weed common on the coast are of a bright pink variegated with brown, throughout which, however, the typical bands and silver spots are retained."

Colour in formalin. Body uniformly yellow, fins hyaline.

Fin counts. The counts made on the single Western Australian specimen were D. iii, xxviii, 2; A. ii, 21; P. 12; V. (i), 2; C. 11 (9+2).

These counts are within the ranges given by McCulloch (1908).

Distribution. Australia: New South Wales (McCulloch 1929), southern Queensland (Whitley 1941), Western Australia.

This is the first record for Western Australia.

***Petraites equiradiatus* Milward, 1960**

Petraites equiradiatus Milward, 1960, West. Aust. Nat., 7, no. 5, p.134.

Material examined. 4 specimens, 73, 74, 83 and 97 mm in total length. Rottnest I., -ii.57 P4472 IB5164, 10.iii.61 P4973 (2).

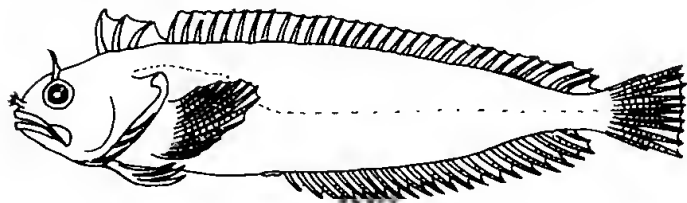


Figure 4.—*Petraites equiradiatus* Milward, P4472, male, 97 mm, Rottnest I., -ii.57.

Description. Body fairly elongate. Snout rounded. Nasal cirrus multifid, with 8 or 9 filaments. Supra-orbital tentacle with a long, tapering outer filament and one or two short inner ones, all broadly joined at base. First three dorsal spines about equal in length, very slightly longer than those following from which they are separated by a gap approximately equal to 3rd spine when depressed; 1st spine just before vertical from margin of pre-operculum; 3rd spine joined by membrane to basal portion of 4th, which is placed over hind border of operculum. First and 2nd dorsal rays more widely spaced than 2nd and 3rd; 3rd ray entirely connected to whole of caudal peduncle by membrane. Anal fin commences beneath 12th dorsal spine. First anal spine about two-thirds length of 2nd; rays increasing very slightly in length to penultimate, the last shorter and connected only basally to peduncle by membrane. Pectoral fin rounded. Ventral fin with a concealed spine and three similar finger-like rays; middle ray a fraction longer than other two, reaching approximately half-way to vent. Caudal fin truncate. Lateral line distinct anteriorly as a series of closely-set tubed scales extending over about two-thirds of the pectoral fin, the series then descending to mid-line and continuing to tail, becoming more widely spaced and less obvious.

Colour in life: Not seen alive.

Colour in formalin. Fairly uniform yellow, except for paler abdomen. Faintest suggestion of seven darker yellow bands on upper sides.

Colour in alcohol. Ground colour yellow-orange. Seven darker, orange-brown, irregular bars on body. Dark brown spots on body, mainly bordering bars. In one specimen lighter bars between the more pronounced ones and a few

spots on the head. All fins hyaline, except for slight brown colouring of membrane basally in dorsal fin above body bars.

Fin counts. The numbers of spines and rays in the 4 specimens examined were D. iii, xxviii-xxix, 3; A. ii, 20-21; P. 12; V. (i), 3; C. 9+2.

Distribution. Known only from Rottnest Island, Western Australia.

***Petraites heptaeolus* Ogilby, 1885**

Petraites heptaeolus Ogilby, 1885, Proc. Linn. Soc. N.S.W., 10, p.225.

Cristiceps wilsoni Lucas, 1891, Proc. Roy. Soc. Vict., (n.s.), iii, p.10.

Material examined. 5 specimens, varying in total length from 44 to 81 mm. Triggs I. 3.iii.56 P6202; Rottnest I. 6.xii.35 P1504-5, 20.iii.58 P6200, 1.iv.56 IB5151.

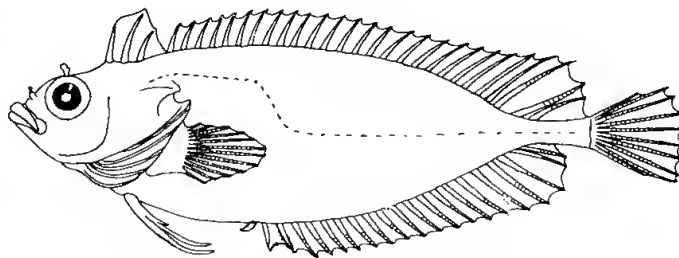


Figure 5.—*Petraites heptaeolus* Ogilby, P6200, male, 70 mm, Rottnest I., 20.iii.58.

Description. Body moderately elongate, laterally compressed. Eyes large, diameter greater than length of pointed snout. Nasal tentacle a short, tubular pedicel bearing a small, ovate cirrus. Supra-orbital tentacle a short, rounded flap. First dorsal spine over pre-opercular margin, forming with 2nd and 3rd a crest slightly higher than remainder of fin; membrane from 3rd spine reaching to base of 4th. Margin of long dorsal fin more or less horizontal, last spine about twice length of anterior ones; 1st ray longer than last spine and widely separated from 2nd ray by clear membrane; 2nd and 3rd rays close together, 3rd joined entirely to whole of caudal peduncle by membrane. Two anal spines stout and shorter than rays, which are equally spaced and increase slightly in length to third last, which is more widely separated from the shorter last two. Pectoral fin rounded, barely or not reaching origin of anal fin. Ventral fin of a concealed spine, two long rays the outer longer, and a short inner ray. Caudal fin sub-truncate, with stout inner rays, and a short, slender one above and below. Lateral line a series of tubed scales, commencing above operculum and running horizontally to just before vertical from vent, where it drops obliquely to mid-line and continues to tail.

Colour in life. Not seen alive. Scott (1962), for South Australian specimens, says "Colour bright olive-green above, lighter below. About seven broken dark bars on the side, extending on to the dorsal fin. Operculum and under parts of head pinkish. Some specimens with a small silver spot behind the eye."

Colour in formalin. Fairly uniform yellow to brown colour.

Fin counts. The numbers of fin spines and rays in the 5 specimens examined were D. iii, xxiv, 1+2; A. ii, 17-18; P. 12; V. (i), 3; C. 8+2.

The counts lie within the ranges, but at the lower extremes, of those given by McCulloch (1908) for New South Wales and Victorian specimens, D. iii, xxiv-xxviii, 1+2; A. ii, 17-21. Scott (1965), for two Tasmanian specimens, gives a pectoral fin ray count of 11 but each of the Western Australian specimens had 12, in agreement with the type description by Ogilby (1885). The suggestion by Scott that the original description giving V. i, 3 was in error, seems to be incorrect, since dissection of Western Australian specimens has shown the spine to be present, although much reduced and concealed.

Distribution. Australia: New South Wales, Victoria (McCulloch 1929), Tasmania (Scott 1965), Western Australia.

Although one specimen was collected at Rottneest Island on December 6, 1935, this is the first published record for the State.

***Petraites antinectes* (Gunther), 1861**

Cristiceps antinectes Gunther, 1861, Cat. Fish. Brit. Mus., iii, pp.273 and 562.

Cristiceps phillipi Lucas, 1891, Proc. Roy. Soc. Vict., (n.s.), iii, p.11.

Petraites antinectes; McCulloch, 1929, Mem. Aust. Mus., 5, p.349.

Material examined. 15 specimens, varying in total length from 33 to 86 mm. Triggs I. 13.iii.56 P6193, 25.xi.57 P6764; North Beach 22.vi.37 P1790; Rottneest I. 18.i.54 P10096(2), 19.i.54 P6194, 21.i.54 P6762, 16.ix.56 P6192, 6.iv.58 P6195-8; Leighton 20.i.56; Cowaramup Bay 11.xi.56 P10382; Cape Leeuwin 30.iii.59 P4467.

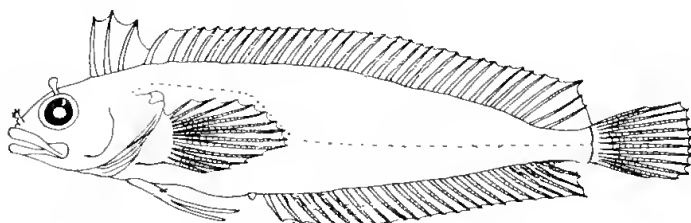


Figure 6.—*Petraites antinectes* (Gunther), P6197, male, 68 mm, Rottneest I., 6.iv.58.

Description. Body fairly elongate. Eyes large. Snout pointed. Lips reach to posterior margin of eye. Nasal cirrus a few short filaments borne palmately on a short, tubular pedicel. Supra-orbital tentacle short and rounded, often with irregular margin. First three spines of dorsal fin form a crest, slightly higher than remainder of fin; 1st spine just in front of vertical from pre-opercular margin; membrane in crest extends slightly beyond spines and from 3rd spine to part-way up 4th. Margin of long dorsal fin fairly uniformly straight; rays equally spaced, last entirely connected to whole of caudal peduncle by membrane. Anal spines shorter than rays, which are longest posteriorly; last ray joined only basally to peduncle by membrane. Pectoral fin extends to or just beyond origin of anal fin. Ventral fin of a

concealed spine, two slender outer rays, the median longer, free for about half their length, and a short inner ray. Caudal fin sub-truncate, with stout inner rays and a short slender one above and below. Lateral line a series of tubes, commencing over operculum and extending roughly parallel to back for a short distance, then approximately over the vent dropping obliquely to mid-line, whence it continues to tail.

Colour in life. Extremely ornate. The ground colour and more intense markings of spots and bars very variable, from light brown to greenish brown and purple. A series of six or seven vertical bars on the body. These bars are widest dorsally and extend onto dorsal fin. They are connected by a horizontal band along the mid-line in some specimens and are edged with thin white lines, that are continuous dorsally but broken ventrally. Paler areas lie between the bars, with silvery spots just below mid-line in most specimens. A 'hammer shaped' marking on caudal peduncle. Abdominal area white, and white spots on lower parts of head and jugular region. A dark spot before eye and a larger one behind it. First three dorsal spines in crest may be dark, with markings extending from them onto head. Long dorsal fin has, in addition to extensions of body bars, spots forming faint horizontal or slightly oblique stripes. Anal fin with a series of spots or bars, each alternate one adjacent to a bar on body. Dark spots on pectorals form lines when rays closed together. Similarly spots form vertical bands on caudal fin. Dark spots also present on ventral fin rays.

Colour in formalin. Bright yellow-orange or brown. The fasciated pattern of life only just evident in most specimens as slightly darker markings on sides of body, and on dorsal and anal fins.

Fin counts. The counts from the 15 specimens examined were D. iii, xxix-xxxi, 3-4; A. ii, 21-22; P. 13; V. (i), 3; C. 10+2. (Note: one specimen had 11 and another 14 rays in the left pectoral fin but both had the usual 13 in the right fin.)

Gunther (1861) initially diagnosed *antinectes* as a variety of *Cristiceps argentatus* Risso, on the grounds of the Australian specimens having a higher anal fin count, ii, 23, than the European and African individuals of the species. Macleay (1882) listed *antinectes* from Western Australia giving the counts D. iii, xxx, 4; A. ii, 23; V. i, 2, but these were almost certainly, together with the description, taken from Gunther's catalogue and not from new material. Whitley (1945) examined the Australian specimens in the British Museum collection and selected a lectotype of *antinectes* having D. iii, xxix, 4; A. ii, 23.

The lower anal fin counts of the specimens now reported upon, five of ii, 21, ten of ii, 22, are, therefore, of note and make it questionable whether Gunther would have recognised a different variety if this material had been available to him. It is further to be noted that Smith (1945, 1953) does not record *argentatus* from South Africa and as the Mediterranean is outside the otherwise known limits of these

fishes, and Whitley does not mention having seen European specimens, the author queries whether or not Risso's material might not have been of Australian origin. If this should prove to be the case *antinectes* would be synonymous with *argentatus*.

Counts recorded under *phillipi* from Victoria and Tasmania by Lucas (1891), McCulloch (1908), and Scott (1966) lie within the ranges D. iii, xxx-xxxii, 2-3; A. ii, 22-25. The differences between these and the counts from Western Australian specimens may be attributed to geographical variation, the author concurring with Whitley (1945) on *phillipi* being synonymous with *antinectes*. Scott (1966) also gives different pectoral and caudal fin ray counts, each of 11, for three Tasmanian specimens.

The ventral fin count, when recorded, has invariably been given as i, 2 or 2. In the Western Australian specimens the inner ray is very small compared with the long, outer ones and it is possible that it has been overlooked or not recorded by other workers.

***Petraites roseus* (Gunther), 1861**

Cristiceps roseus Gunther, 1861, Cat. Fish. Brit. Mus., iii, p.274.

Petraites roseus; Waite, 1904, Rec. Aust. Mus., 5, pp.181 and 224.

Petraites sellularius Whitley, 1931, Aust. Zool., 6, p.323.

Note on synonymy. Gunther described the species from the coasts of Australia and New Guinea but the latter locality is extremely unlikely from our knowledge of the distribution of the genus. Whitley (1931) separates the New South Wales and Lord Howe Island forms from *P. roseus*, since they differ from Gunther's description in having the height $4\frac{1}{2}$ in total length (Gunther: 5) and eye longer than the snout (Gunther: equal). The allometric growth of these fishes, however, makes these poor diagnostic characters. An examination of Western Australian specimens has revealed much variation in these and other proportions depending on the size of the fish.

Material examined. 9 specimens, varying in total length from 31 to 145 mm. Lancelin I. 23.i.58, 7.iv.58; Rottnest I. 18.i.54 P10094, 20.iii.58 P6199, 23.viii.58 IB5200; Cottesloe 24.vii.23 P885-6; Cowaramup Bay 11.xi.56 P10381; Walpole Inlet 9.vii.49 P3257.

Description. Body moderately elongate, laterally compressed and increasing in depth with growth. Eyes large. Snout pointed. Lips extending to or just beyond posterior margin of eye. Nasal cirrus a few short filaments borne on a short, tubular pedicel. Supraorbital tentacle about equal to diameter of eye in height, with outer border entire but top and inner side dissected forming an irregularly

TABLE 2
Reproductive condition of females

								Ovarian Contents			
				Month Collected		Locality		Oocytes or Eggs with No Visible Development		Developing Embryos	
<i>C. australis</i>											
1.	104 mm	April	Albany	—
2.	166 mm	April	Albany	+
3.	191 mm	May	Rockingham	+
4.	137 mm	July	Coogee	+
5.	148 mm	July	Cottesloe	—
6.	161 mm	August	Albany	+
7.	216 mm	September	Albany	+
8.	133 mm	October	Cape Bouvard	+
9.	136 mm	October	Cape Bouvard	+
10.	143 mm	October	Cape Bouvard	+
<i>C. aurantiacus</i>											
1.	161 mm	April	Geraldton	—
2.	208 mm	September	Point Peron	+
3.	210 mm	October	Geraldton	+
4.	244 mm	October	Point Peron	+
<i>P. nasutus</i>											
1.	49 mm	January	Rottnest I.	+
<i>P. heptaeolus</i>											
1.	81 mm	March	Triggs I.	—
<i>P. antinectes</i>											
1.	86 mm	January	Rottnest I.	+
2.	60 mm	January	Rottnest I.	+
3.	48 mm	April	Rottnest I.	+
4.	43 mm	November	Cowaramup Bay	—
<i>P. roseus</i>											
1.	116 mm	August	Rottnest I.	+

+ = present

— = absent

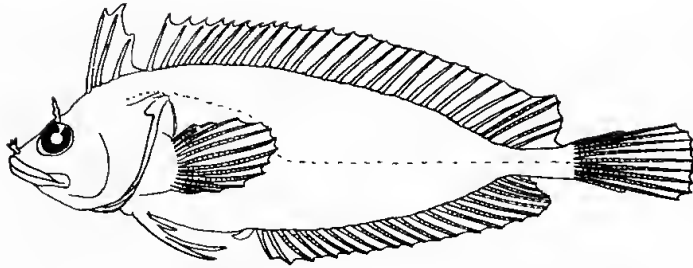


Figure 7.—*Petraites roseus* (Gunther), P6199, male, 78 mm, Rottnest I., 20.iii.58.

lobate margin. First dorsal fin spine just behind eye, forming with 2nd and 3rd a crest higher than remainder of fin; membrane of crest produced beyond spines; membrane from 3rd spine just reaches base of 4th. Spines of long dorsal fin increase in length posteriorly; rays irregularly spaced, last entirely connected to whole of caudal peduncle by membrane. Anal spines shorter than rays, which are longest posteriorly; membrane from last ray united to about halfway along peduncle. Pectoral fin rounded, extending to or just beyond origin of anal fin. Ventral fin of a concealed spine, two long, sub-equal, stout rays and a short, slender inner one. Caudal fin sub-truncate, with strong inner rays and a shorter, slender one above and below.

Colour in life (of specimen 31 mm long, from Cowaramup Bay). Uniformly dark brown over all body and head. A distinctive gold speck just behind eye. Two sections of clear membrane at posterior end of dorsal fin.

Colour in formalin. Fairly uniform yellow-orange. Suggestion of darker orange bars on body, dorsal and anal fins, and rows of orange spots on caudal fin rays in some specimens.

Fin counts. The numbers of fin spines and rays in the 9 specimens examined were D. iii, xxv-xxvii, 3-4; A. ii, 19-21; P. 12; V. (i), 3; C. 9+2.

These counts lie within the ranges given by Macleay (1882) and McCulloch (1908) for New South Wales and Lord Howe Island specimens, with the exception of the count of 27 spines in the 2nd dorsal fin, which was present in 2 specimens, one of 130 mm from Rottnest Island and one of 31 mm from Cowaramup Bay.

Distribution. Australia: Western Australia, New South Wales (McCulloch, 1929), Queensland (Marshall, 1957). Lord Howe Island (Ogilby, 1889).

Notes on Biology

Habitats and habits. *Cristiceps australis* and *C. aurantiacus* are known mainly from sea-grass beds. These sea-grasses, of the genera *Posidonia*, *Cymodocea*, *Zostera*, and *Halophila*, form extensive beds along much of the coastline, where sand deposits are fairly fixed and stable.

Both species range from the sea-grass beds in shallow waters close inshore into waters at some depth. *C. aurantiacus* extends at least to seventeen fathoms, two specimens having been taken at this depth in a crayfish-pot.

All the specimens of *Petraites* were collected from close inshore in shallow water, with one exception, a *P. roseus*, which was from a crayfish-

pot at seventeen fathoms. North of Cape Naturaliste most were found on aeolianite erosion platforms. South of this point they occur also on igneous rock benches.

Both *Cristiceps* species swim freely away from the bottom but are also able to move in contact with the substratum, employing the pelvic fin rays in the manner of walking legs. Their coloration and the slow undulatory movements of body and fins when swimming make them extremely difficult to detect amongst the sea-grass fronds.

The available evidence suggests that in the daytime the inshore individuals of the *Petraites* species remain relatively dormant, hidden amongst algae and in pools on the platforms, and possibly also in the deeper sub-littoral, becoming more active and feeding during darkness.

Food. Analyses of stomach and intestinal contents indicate that the *Cristiceps* spp. and *P. antinectes* and *P. equiradiatus* are carnivorous. Specimens of the other *Petraites* spp. examined contained no food.

Cristiceps specimens contained crustaceans, mainly amphipods, and fishes. Their ability to take large food was shown by a specimen of *C. aurantiacus*, measuring 210 mm, which contained a semi-digested piece of fish (only the tail from the anal origin backwards) 43 mm in length and with vertebral spines 11 mm long.

Crustaceans appear to be the principal food of *P. antinectes* and *P. equiradiatus*, the specimens examined containing large numbers of these but no other organisms.

Reproduction. All the Western Australian clinids are ovo-viviparous, development of the embryos occurring within the ovarian cavity. Males possess a tapered, forwardly curved, genital phallus.

The ovaries of female specimens were examined to determine the presence or absence of embryos. The results are given in Table II. From the table it may be seen that breeding appears to take place during most months of the year. Certainly there is no restricted period during which all the fishes carry and produce the young. In this the Western Australian species differ from those in South Africa, where, according to the statement by Smith (1958)—“large numbers of young being born August-October”—there is a definite breeding season.

It has also been discovered that in some at least of the Australian species, viz. *Cristiceps australis*, *Petraites nasutus*, *P. antinectes*, more than one brood of embryos may develop simultaneously within the ovaries. Thus, in addition to the various sized oocytes normally present, there can be one or more distinct groups of embryos. In one specimen of *C. australis* examined from Moreton Bay, Queensland, and measuring 156 mm, four broods at clearly separated stages of development were present. This occurrence of multiple broods, i.e. superfoetation, the term used by Turner (1937) in reference to poeciliid fishes, has not previously been recorded in the Blennioidea and is being further investigated.

From the evolutionary view-point it is to be noted that all the American clinids are oviparous. Ovo-viviparity originated within the family following dispersal of representatives to the South African region. In the Australian forms the trend has progressed further, with an apparent lengthening of the breeding season and the development of superfoetation.

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2.—The genus *Sphenomorphus* (Lacertilia, Scincidae) in Western Australia and the Northern Territory

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Abstract

Mittleman's concept of *Sphenomorphus* has been amended by including certain species that he placed in *Lygosoma* and by excluding species recently transferred to *Ctenotus*. The following species and subspecies are defined and keyed: *richardsoni* Gray (including *monotropis* Boulenger and *ambiguus* De Vis), *f. fasciolatus* Günther (including *intermedius* Sternfeld), *f. pallidus* Günther, *i. isolepis* Boulenger (including *forresti* Kinghorn), *i. douglasi* nov., *australis* Gray (including *gracilipes* Steindachner but not "*Sphenomorphus australis* (Gray)" of Loveridge), *crassicaudus arnhemicus* nov., and *c. darwiniensis* nov. A neotype has been proposed for *Lygosoma australis* Gray.

Introduction

Under the long-forgotten but older name *Sphenomorphus*, Malcolm Smith (1937) restricted Boulenger's (1887) concept of *Hinulia* by removing several southeast Asian species to the revived genus *Otosaurus*, and broadened it by including certain weak-limbed (but pentadactyl) skinks that had been wrongly placed in *Omolepida*. Smith's treatment of the Australian "Omolepida" was not consistent: *australe* alone was placed in *Sphenomorphus*; the closely related *crassicaudum* was transferred to *Ictiscincus*, and *pumilum*, *punctulatum* and *mjobergi* to *Lygosoma*.

Mittleman's (1952) concept of *Sphenomorphus* was generally similar to Smith's. His main departure was to synonymise *Ictiscincus* with it; *crassicaudum* was thus transferred to *Sphenomorphus*, while its relatives, *punctulatum* etc., remained segregated in *Lygosoma*.

As the present paper is only concerned with part of the range of *Sphenomorphus*, my views on the limits of the genus are not relevant here. However, several species included in *Hinulia* by Boulenger, and in *Sphenomorphus* by both Smith and Mittleman, were recently transferred to *Ctenotus* (Storr 1964).

* Neither of these authors cites the authority for this designation. The choice was ill-advised but evidently valid. The biological species *quoyi* was not among the several species originally included by Gray in *Hinulia*. However the nominal species *quoyi* was among them by virtue of Gray's placing it in the synonymy of *Tiliqua reevesi*, an included species. That Gray's synonymy was grossly erroneous, is irrelevant according to my reading of the Code (1961: 69).

Elania J. E. Gray, 1845, 'Cat. Specimens Liz. Brit. Mus.', p.80. Type-species: *Scincus muelleri* Schlegel [by monotypy].

Ictiscincus M. A. Smith, 1937, Rec. Ind. Mus. 39: 22. New name for *Elania* Gray.

The following survey was based on material in the Western Australian Museum (numbers prefixed with R), in the collections of the Animal Industry Branch, Northern Territory Administration, Alice Springs (numbers prefixed with NTM), in the collection made by W. H. Butler jointly for the W.A.M. and A.M.N.H. (indicated by WHB), and in the South Australian Museum (number prefixed with SAM).

Genus *Sphenomorphus* Fitzinger

Sphenomorphus Fitzinger, 1843, 'Systema Reptilium', p.23. Type-species: *Lygosoma melanopogon* Duméril & Bibron [fide Smith (1937) and Mittleman (1952)].

Eulamprus Fitzinger, 1843, 'Systema Reptilium', p.22. Type-species: *Lygosoma quoyi* Duméril & Bibron [fide Smith (1937) and Mittleman (1952)].

Hinulia J. E. Gray, 1845, 'Cat. Specimens Liz. Brit. Mus.', p. 74. Type-species: *Lygosoma quoyi* Duméril & Bibron [fide Smith (1937)* and Mittleman (1952)*].

Diagnosis. Limbs pentadactyl. Tail fragile, longer than head and body. No supranasals. Eyelid moveable, without a transparent disc. Tympanum sunken. Parietals in contact behind interparietal. Distinguishable from *Ctenotus* by thick tail, swollen supraocular region, absence of auricular lobules and of bold longitudinal striping, and crepuscular (if not nocturnal) way of life.

Distribution. From tropical Africa through southern Asia to Australia and New Zealand.

General description (of species in this paper). Habitus small to moderately large, elongate or stout. Limbs weak to moderately strong, adpressed hind-leg never reaching to axilla and sometimes falling far short of it. Digits not or slightly compressed, short to moderately long, each bearing a long, sharp claw. Ear aperture smaller than eye, with or without granules projecting back from anterior margin. Tail (when original) 1.3-1.9 times as long as head and body, but usually regenerated.

Frontonasal invariably in contact with rostral and nearly always with frontal. Prefrontals well developed. Frontal long and narrow, kite-shaped with long sides concave, about as long as frontoparietals and interparietal together, considerably narrower than supraocular region. Frontoparietals paired, longer or shorter than free interparietal. Supraoculars 4; first two broadly, and third not or very narrowly, in contact with frontal. Supraciliaries 5-9, first invariably largest. Loreals 2, posterior larger. Preoculars 2, lower larger. Suboculars 4 or 5, anterior two or three separated from posterior two by third-last labial. Temporals normally

3; single primary smallest; upper secondary oblong, much longer than wide, broadly in contact with parietal; lower secondary about as large as last two labials, its posterior edge broadly in contact with long, vertically narrow scale that Copland (1945) calls a tertiary temporal (it is probably formed by fusion of two transversely adjacent lateral scales, in same way as enlarged nuchals). Upper labials 6-9; last two largest; third-last alone entering orbit (second-last and fourth-last precluded by posterior and anterior suboculars respectively). No occipitals. Nuchals 0-4 on each side (including large oblique scales bordering parietal, as well as dorsal scales transversely enlarged by fusion of anteriormost vertebrae with adjacent paravertebrals). Midbody scales in 19-36 longitudinal rows; dorsals smooth or obtusely uncarinate. Two preanal scales slightly to moderately enlarged. Subdigital lamellae entire or divided, smooth or weakly keeled. 15-29 under fourth toe.

Key

- | | | |
|----|--|---------------------------|
| 1. | Midbody scale rows more than 24; adpressed limbs overlapping or failing to meet by less than length of fore-leg | 2 |
| | Midbody scale rows fewer than 24; adpressed limbs failing to meet by more than length of fore-leg | 6 |
| 2. | Supracaudals (and often dorsals) keeled; dorsum and/or sides banded with dark brown | 3 |
| | Supracaudals and dorsals not keeled; dorsum and/or sides spotted with dark brown; sutures between upper labials broadly margined with dark brown | 5 |
| 3. | Bands on back and tail sharply defined, as broad or almost as broad as pale interspaces, fewer than 13 on body and 30 on tail; upper labials usually 8 | <i>S. richardsoni</i> |
| | Bands on back and tail much narrower than pale interspaces, more than 10 on body and 30 on tail; upper labials usually 7 | 4 |
| 4. | Bands more conspicuous on back than on flanks | <i>S. f. fasciolatus</i> |
| | Bands less conspicuous on back than on flanks | <i>S. f. pallidus</i> |
| 5. | Broad blackish dorsolateral streak on anterior part of body, usually dotted with white; upper labials usually 6 | <i>S. i. douglasi</i> |
| | No anterior dorsolateral streak (if dark spots are concentrated dorsolaterally it is for whole length of body and never so densely as to form solid streak); upper labials usually 7 | <i>S. i. isolepis</i> |
| 6. | Flanks spotted with white; 3 anterior suboculars; usually 6 postoculars | <i>S. australis</i> |
| | Flanks not spotted with white; 2 anterior suboculars; usually 5 postoculars | 7 |
| 7. | Dorsum unstriped, dotted with dark brown, not sharply demarcated from densely spotted sides; more than 18 lamellae under fourth toe | <i>S. crassicaudus</i> |
| | Broad pale brown paravertebral stripe, sharply demarcated from dark flanks and vertebral stripe; fewer than 18 lamellae under fourth toe | <i>S. c. darwiniensis</i> |

Sphenomorphus richardsoni (Gray)

Hinulia richardsonii J. E. Gray, 1845, 'Cat. Specimens Liz. Brit. Mus.', p.271. Houtman Abrolhos, Western Australia (B. Bynoe).

Lygosoma monotropis Boulenger, 1887, 'Cat. Liz. Brit. Mus.' 3: 237. Champion Bay, Western Australia (F. H. du Boulay).

Hinulia ambigua De Vis, 1888, Proc. Linn. Soc. N.S.W. (2) 2: 817. Charleville, Queensland.

Diagnosis. Moderately large and stout *Sphenomorphus* whose adpressed limbs overlap or fail to meet by less than length of fore-leg. Distinguishable from *S. isolepis* by keeling of supracaudals (and often of dorsals) and by numerous dark bands across body and tail, and from *S. fasciolatus* by bands across body and tail being fewer and about as wide as pale interspaces.

Distribution. Western Australia from south Kimberley and Warburton and Blackstone Ranges south to Wheat-Belt, Eastern Goldfields and Nullarbor Plain; east through northern South Australia to southwestern Queensland.

Description. Fore-leg 22-33 (av. 27.2) and hind-leg 29-45 (36.8) % of SVL (snout-vent length). Digits moderately long and slender, moderately or weakly compressed; fourth finger slightly longer than third. Tail 1.32-1.71 (1.52) times as long as SVL in the few (ca 20%) specimens with original tail. Ear aperture vertically elliptical or subcircular, about half as large as eye, margined anteriorly with 0-4 granules. Maximum SVL 113 mm.

Nasals usually widely (rarely narrowly) separate. Prefrontals usually narrowly separate, rarely widely separate or just touching or forming very short common suture. Frontal usually in contact with first three (sometimes two) supraoculars; usually a little longer (occasionally as long as but never shorter) than combined length of frontoparietals and interparietal; abnormally divided transversely and longitudinally. Frontoparietals usually shorter (occasionally longer) than interparietal. Supraciliaries 7-9. Temporals normally 3, abnormally 4 due either to vertical division of a secondary or to horizontal division of last labial. Upper labials usually 8 with four wholly and fifth partly anterior to orbit; occasionally 7 or 9 due to fusion or division in anterior labials. Enlarged nuchals 0-4. Midbody scales in 28-34 rows; laterals smallest, ventrals largest; dorsals subequal, weakly and obtusely uncarinate or almost smooth. Keels of supracaudals a little stronger and sharper than those of dorsals and similarly aligned longitudinally. Lamellae under fourth toe 21-29 (24.3), divided (except distal 3-10), each semilamella tuberculately keeled (keels strongest proximally, occasionally sharper distally), undivided lamellae smooth or very weakly keeled.

Upper surface pale yellowish brown with 8-13 (9.9) moderately broad, irregular (but sharply defined) dark brown bands across body and 19-29 (22.6) across tail (regenerated tails are uniformly brown); bands as wide as or a little narrower than pale interspaces, sometimes ending at midline or branching to form a Y or X; bands darker in juveniles than adults. Under surface whitish except for palms, soles and under digits, which may be greyish.

Geographic variation. This species is widely distributed in arid and semiarid parts of Western Australia between latitudes 18 and 32° S. There is no geographic variation in colour pattern, and only a slight amount in meristics, proportions and scutation, which, apart from the Kimberley-Pilbara population, only became apparent when the data were broken down geographically.

(1) *Kimberley-Pilbara*: 13 specimens from between Halls Creek and Tambrey. The most distinctive population, and especially characterised by (a) large size (SVL exceeding 100 mm in 7 specimens, whereas no specimen from other populations attains more than 97); (b) reduced keeling (dorsal scales virtually smooth); (c) few nuchals (averaging 0.6 on each side, against 0.9-1.2 in other populations), (d) high frequency of frontoparietals longer than interparietal (45%, against 0% in neighbouring Mid-west Coast and Western Interior populations, and 20-23% in others). Additionally, it shares with Mid-west Coast and Western Interior populations high number of upper labials (mainly 8, occasionally 9, never 7; against mainly 8, occasionally 7, never 9 in others).

(2) *Mid-west Coast*: 8 specimens from between Yardie Creek and Warroora. Especially characterised by low number of midbody scale rows (28-32, av. 30.1; against averages of 30.6-33.3 in others) and relatively strong dorsal keeling.

(3) *Western Interior*: 15 specimens from between the upper Gascoyne and Paynes Find. This population has no peculiarities and is intermediate between the first two, but nearer to the second, with which it shares the distinction of having the interparietal always longer than frontoparietals. Poorly differentiated from South-west and North-east populations.

(4) *South-west*: 20 specimens from Ajana south and east to Narrogin and Woolgangie. Another poorly differentiated population. Limbs relatively shorter and size probably less than in other populations (no specimen has SVL > 86).

(5) *Eastern*: 13 specimens from Wiluna south and east to the Goldfields and Nullarbor Plain. Their main peculiarities are (a) 58% of specimens have only two supraoculars in contact with frontal (against 0-32% in other populations); (b) 23% have frontal not clearly longer than frontoparietals and interparietal together (against 0-12% in others); and (c) more numerous lamellae under fourth toe, viz. 23-29 (25.8), against averages of 22.8-24.5 in others.

(6) *North-east*: 15 specimens from Warburton and Blackstone Ranges. Their only peculiarity is the low number of lamellae under fourth toe, viz. 21-26 (22.8), against averages of 24.0-25.8 in others.

Some of the geographic variation in *S. richardsoni* seems to be clinal, e.g. decrease in absolute size and relative length of limbs from north to south; increase in number of enlarged nuchals from north to south; increase in number of midbody scale rows (and possibly also strength of dorsal keeling) from the mid-west coast through the western interior to peripheral populations; and decrease in number

of upper labials from northwest to southeast. Other characters, like the number of dorsal bands, supraciliaries and subdigital lamellae, and the frequency of frontoparietals longer than interparietal and of two rather than three supraoculars in contact with frontal, vary irregularly, which indicates some regional restriction in gene-flow.

Remarks. While there is clearly some geographic variation in *S. richardsoni*, it is doubtful whether any of it amounts to subspeciation. The only possible exception is the Kimberley-Pilbara population; but before considering this a distinct subspecies, more should be learnt of its relationship to neighbouring populations. No specimen has yet been taken in the 240-mile gap between Tambrey and Yardie Creek or in the 170-mile gap between Woodstock and Mt. Newman. A single specimen from the latter locality differs from Pilbara specimens and agrees with the Mid-west Coast series in its low number of midbody scale rows (29) and relatively strong dorsal keeling. Another difficulty to be resolved before formally recognising the Kimberley-Pilbara population is the questionable type-locality of *richardsoni* (see below).

The Mid-west Coast series, better than any other, fits the original description of *monotropis*; whereas our single topotype from Geraldton (which was grouped above with the South-west population) has weakly keeled dorsals, 34 rows of midbody scales and four auricular granules. This Geraldton specimen is evidently less like the type of *monotropis* than that of *richardsoni*, which brings us to the question of the latter's type-locality.

The type of *richardsoni* was originally stated by Gray as coming from the Houtman Abrolhos. Yet these islands have been worked this century by several expeditions, which have all failed to collect *richardsoni* and several other reptiles and amphibia supposed to occur there (Storr 1965). All of these problematic species have been found on the opposite mainland, and it is possible that the early collectors (generally notorious for their imprecise or erroneous locality data) did not distinguish between insular and continental collections. If in fact *richardsoni* was obtained on the opposite mainland, at or near Champion Bay, it would be an absolute synonym of the junior *monotropis*. The smooth dorsals, possibly correlable with large size, are the greatest difference between the type of *richardsoni* and our Geraldton specimen. If on the contrary it were demonstrable that southern animals never have the dorsals so smooth or attain a snout-vent length of 127 mm, the possibility would have to be considered that the type of *richardsoni* really came from the Pilbara or further north.

At present it would be premature to correct the type-locality of *richardsoni*. Nor will it become urgent to do so, while there is no good reason for formally dividing the western populations.

Two juveniles from Lanbinna (west of Oodnadatta, S.A.) are tentatively placed with *richardsoni* because of their relatively broad

and irregular caudal bands and eight upper labials. Nevertheless they are not very different from Alice Springs specimens of *fasciolatus*, with which they agree in having 12-14 dorsal bands. They share with the Eastern (W.A.) population of *richardsoni* high number of subdigital lamellae (25-26); moreover one of them has only two supraoculars in contact with the frontal, and neither has the frontal clearly longer than frontoparietals and interparietal together. In addition to being intermediate between the Eastern (W.A.) population of *richardsoni* and the Southern (N.T.) population of *fasciolatus*, they are unique in having banded legs.

De Vis separated his *ambiguus* from *richardsoni* because of its "larger scales, shorter body, and longer limbs". His single specimen had 32 rows of midbody scales, and limbs 27 and 38% of SVL (52 mm), which is well within the variation of *richardsoni*. Likewise the 9 dorsal bands "nearly as broad as the intervals" and 27 caudal bands place it with *richardsoni*. Loveridge (1934 : 354) synonymised *ambiguus* with *fasciolatus*, apparently because of his belief that *fasciolatus* and *monotropis* were western and eastern (rather than northern and southern) representatives.

Material examined. *Kimberley Division* (W.A.): SAM 3535 (Moola Bulla, 12 mi. W of Halls Creek); WHB (1) (Mt. Phire, 20 mi. E of Anna Plains). *North-West Division* (W.A.): R 11087 (Abydos); R 13095-6, 13313, 17891-4, 25103-4 (Woodstock); R 1390 (Tambrey); WHB (1), R 13269-70, 15127 (Yardie Creek); R 8212-3, 8232 (Warroora); R 23990 (Mt. Newman); R 6463 (upper Gascoyne); R 15779-81 (Mileura); R 7369 (Belele); R 7368 (Meekatharra); R 1521 (Wurarga); R 4595-6 (Gullewa); R 7513 (Muralgarra); R 13971, 13974 (Burnabinmah); R 12644 (Paynes Find); WHB (1) (12 mi. NE of Rothsay). *South-West Division* (W.A.): R 25218 (Ajana); R 8595 (Geraldton); R 4624 (Koolanooka); R 3848 (Mogumber); R 1502 (Koorda); R 4567, 10187 (Mukinbudin); R 2833 (Nungarin); R 2419-20 (Meckering); R 2589 (Northam); R 17895 (38 mi. from Perth); R 17900 (Talbert); R 18496 (Boyagin Rock, 10 mi. SW of Brookton); R 8844 (Pingelly); R 17896 (15 mi. E of Pingelly); R 2179 (Wickepin); R 7027 (Narrogin). *Eastern Division* (W.A.): R 20747 (Blackstone Mining Camp); R 14643, 17112, 17745-7, 17855, 22008-10, 22058, 22069-70, 22103, 22200 (Warburton Range); R 6340, 8935 (Wiluna); R 12408, 19768 (Kathleen Valley); R 17897 (Cosmo Newberry); R 1763, 23905 (Laverton); R 12984 (Queen Victoria Spring); R 17898 (6 mi. W of Coonana); R 6390 (Boulder); R 12742-3 (Woolgangie). *Eucla Division* (W.A.): R 17899 (Seemore Downs); R 15210 (Rawlinna). *South Australia*: R 2270 (Ooldea); NTM 1553-4 (Lanbinna).

Sphenomorphus fasciolatus fasciolatus (Günther)

Hinulia fasciolata Günther, 1867, Ann. Mag. Nat. Hist. (3) 20: 47. Rockhampton and Port Curtis, Queensland (G. Krefft).

Lygosoma (Hinulia) fasciolatum intermedium Sternfeld 1919, Senck. Biol. 1: 81. Hermannsburg, Northern Territory (M. von Leonhardi).

Diagnosis. Moderately large *Sphenomorphus* whose adpressed limbs overlap or fail to meet by less than length of fore-leg. Distinguishable from *S. isolepis* by keeling of supracaudals and dorsal pattern of transverse bars (not of spots); and from *S. richardsoni* by more numerous, less regular and narrower body bands, and more numerous, more regular and narrower caudal bands.

Distribution. Interior of Northern Territory between latitudes 15 and 25°S. southeast and east to coast of central Queensland.

Description. Fore-leg 23-29 (26.3) and hind-leg 33-41 (37.3) % of SVL. Digits moderately long and slender, moderately or weakly compressed; fourth finger slightly longer than third. Tail 1.33-1.42 (1.36) times as long as SVL in five (of 16) specimens with original tail. Ear aperture vertically elliptical or subcircular, about half as large as eye, margined anteriorly with 0-3 granules. Maximum SVL 86.5 mm.

Nasals widely separate. Prefrontals usually moderately (sometimes narrowly, rarely widely) separate. Frontal usually in contact with first three (sometimes two) supraoculars, usually a little longer (occasionally as long as but never shorter) than combined length of frontoparietals and interparietal, abnormally divided horizontally. Frontoparietals about as long as interparietal. Supraciliaries 6-8 (7.2). Temporals normally 3; abnormally 2, due to fusion of primary with upper secondary. Upper labials usually 7, with first three wholly and fourth partly anterior to orbit; occasionally 8, due to division of an anterior labial. Enlarged nuchals 0-2 (0.7) on each side. Midbody scales in 30-36 (32.8) rows; laterals smallest; dorsals subequal, weakly and obtusely uncarinate or smooth. Keels of supracaudals a little stronger and sharper than those of dorsals and similarly aligned longitudinally. Lamellae under fourth toe 18-28 (23.1), weakly divided (except distal 6-13), tuberculately keeled.

Upper surface pale brown with 11-19 (13.5) irregular dark brown bands across body, each 1-2 scales wide and separated by pale interspace of 3-5 scales, often broken mid-dorsally (especially on neck), becoming paler, narrower and deflected forwards on flanks; and with 35-40 (37.6) bands on tail, usually very regular (except first 2-3) and occupying a single transverse row of scales and separated by two rows of pale scales. Under surface whitish except under digits, which may be greyish.

Geographic variation (in Northern Territory). As in *richardsoni*, individual variation is greater than geographic variation. The following division of the material reveals some slight regional differentiation.

(1) *North*: 2 specimens from Larrimah. These have the most numerous dorsal bands (17 and 19), fewest subdigital lamellae (18-22), fewest nuchals (0-1, av. 0.5) and relatively smallest limbs and ear aperture.

(2) *Central*: 7 specimens from between latitudes 20 and 22°S. Dorsal bands 12-16 (13.3). Subdigital lamellae 22-28 (24.9). Nuchals 0-1

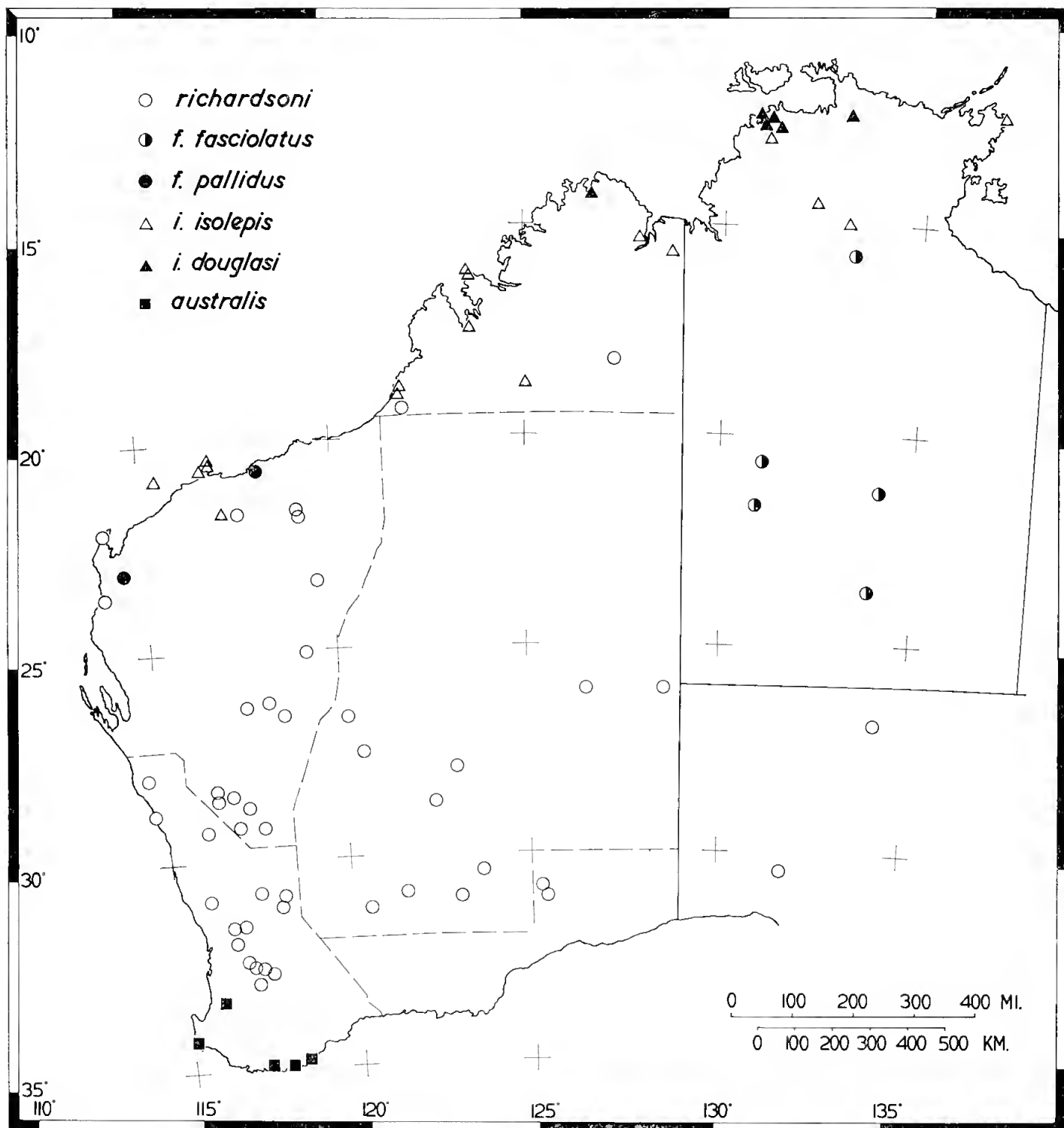


Figure 1.—Map of Western Australia and the Northern Territory showing location of specimens of four species of *Sphenomorphus*.

(0.7). No specimen has frontoparietals longer than interparietal, or upper secondary temporal larger than lower.

(3) *Scuth.*: 7 specimens from Alice Springs and vicinity. Dorsal bands 11-14 (12.4). Subdigital lamellae 20-26 (22.3). Nuchals 0-2 (0.9). Four specimens have frontoparietals longer than interparietal. Two specimens have 8 upper labials (invariably 7 in other populations). Banding in one specimen highly irregular on tail as well as body. Only one specimen has an auricular granule (against 2-3 in a third of the individuals of other populations).

Some of the variation seems to be clinal, e.g. north-south decrease in number of dorsal bands and increase in number of nuchals. Other characters vary irregularly, e.g. number of subdigital lamellae. A third class of variation could be due to past introgression of characters from neighbouring taxa, e.g. 8 labials and irregular caudal banding in some southern specimens (from *S. richardsoni*), and small ear aperture and pale, very irregular dorsal banding in the north (from *S. f. pallidus*).

Remarks. Sternfeld (*supra cit.* and 1924) separated "intermedius" from *fasciolatus* because of supposed differences in size, length of appendages and coloration (intermediate between *monotropis* and *fasciolatus* but nearer to latter). He evidently had no comparative material and relied on descriptions and measurements in Boulenger (1887) for his concepts of typical *fasciolatus* and *monotropis*. Admittedly none of his series (SVL 35-83 mm) was as large as the specimen of *fasciolatus* (SVL 98 mm) measured by Boulenger, but the relative length of the latter's fore-leg and hind-leg (28 and 38% of SVL) fall well within the range of Sternfeld's Hermannsburg series (24-31% and 34-43%). The relatively short tail of the specimen measured by Boulenger could have been regenerated; it is certainly so in the specimen figured by Boulenger.

Material examined. Northern Territory: R 24144-5 (4 mi. S of Larrimah); NTM 2083-6 (Tanami Desert Sanctuary, ca 20°35'S, 131°E); NTM 2693, 2758 (Newnans Cave, 21°38'S, 130°50'E); R 24350 (Taylors Well, 26 mi. NE of Barrow Creek); NTM 1539, 2107-8, 2284-5, 2576, 2896 (near Alice Springs).

Sphenomorphus fasciolatus pallidus (Günther)

Hinulia pallida Günther, 1875, in Richardson & Gray's 'Zool. Erebus & Terror' 2: 12. Nickol Bay, Western Australia (F. H. du Boulay).

Diagnosis. Medium-sized *Sphenomorphus* whose adpressed limbs overlap by less than length of hand. Distinguishable from *S. f. fasciolatus* by obscurity of dorsal banding, depressed snout and very small ear aperture.

Distribution. Northwest coastal plains of Western Australia from Mundabullangana southwest to Marilla.

Description. Fore-leg 25% and hind-leg 38% of SVL. Digits weakly compressed; fourth finger slightly longer than third. Ear aperture subtriangular, $\frac{1}{3}$ as large as eye, not margined anteriorly with granules. SVL 69 mm.

Nasals widely separate. Prefrontals moderately separate. Frontal in contact with first two supraoculars; a little longer than combined length of frontoparietals and interparietal. Supraciliaries 7. Temporals 3, primary smallest, upper secondary largest. Upper labials 7; first three wholly and fourth partly anterior to orbit; last two largest, larger than lower secondary temporal. Enlarged nuchals 0-1 on each side. Midbody scales in 34 rows; ventrolaterals smallest; dorsals largest, subequal, smooth. Supracaudals obtusely unicarinate with keels aligned longitudinally. Lamellae under fourth toe 20-21, weakly divided proximally; each semilamella tuberculately keeled; middle and distal lamellae with a moderately sharp keel.

Upper surface pale greyish brown, banded with slightly darker brown. Dorsal bands obscure, narrow and highly irregular, more distinct and deflected forwards on flanks where 11 are discernible between axilla and groin. Caudal bands distinct and regular, each occupying one transverse row of scales and separated by pale interspace two-scales wide and bearing a fairly regular line of small spots similar in colour to caudal bands. Under surface whitish.

Remarks. Our material agrees fairly well with Günther's description of the type, but not so well with Boulenger's (1887 : 233) with respect to coloration. Perhaps the specimen had faded in the interval between the two descriptions.

While there is little doubt that our specimens* are identical with Günther's *pallidus*, it is another matter whether *pallidus* is worthy of subspecific rank. The differences between these specimens and some examples of *f. fasciolatus* (especially the smaller of the two Larrimah specimens) are trivial and require confirmation with series.

S. fasciolatus and *S. richardsoni* are much more alike than any other two species dealt with here, and Sternfeld (1919, 1924) and Loveridge (1934 : 354) understandably regarded them as conspecific; but whatever happens in the east, they behave as good species in the west of the continent. The distribution of *S. f. pallidus* is entirely surrounded (if not overlapped) by that of *S. richardsoni*, and it is clear that there is no gene-flow between the two. The bold banding and high labial counts of northern *richardsoni* are quite unaffected by the proximity of *pallidus*.

It is possible that *fasciolatus* and *richardsoni* have different habitat requirements. The latter is largely confined to hilly or rocky country and is commonly found under exfoliating granite. The Mundabullangana specimen of *f. pallidus* (like the Larrimah and Taylors Well specimens of *f. fasciolatus*) was taken at a windmill in plain country. No habitat details are available for the Marilla specimen of *pallidus*, but the country round that station consists of plains and sand dunes.

* One of them, R5336 from Marilla, is evidently lost. However, its coloration as described by Glauert (1961: 73) is similar to that of R17060.

I have been unable to locate the Carnarvon specimen referred by Glauert (1961 : 72) to "*Lygosoma pallidum*."

Material examined. North-West Division (W.A.): R 17060 (9 mi. SW of Mundabullangana).

***Sphenomorphus isolepis isolepis* (Boulenger)**

Lygosoma isolepis Boulenger, 1887, "Cat. Liz. Brit. Mus." 3: 234. Nickol Bay (F. H. du Boulay), Swan River and Australia.

Lygosoma (Hinulia) isolepis foresti [sic] Kinghorn, 1931, Rec. Aust. Mus. 18: 358. Forrest River, Western Australia (L. Wood).

Diagnosis.—Medium-sized, somewhat stout *Sphenomorphus* whose adpressed limbs just overlap (juveniles) or fail to meet (adults). Distinguishable from *S. fasciolatus* and *S. richardsoni* by its intensely spotted colour pattern (especially on sides) and smooth supracaudals.

Distribution. Far north of Northern Territory (east to Yirrkala and south to Mataranka, but excluding extreme northwest); Kimberley Division of Western Australia (mainly near coast, but excluding extreme north); and North-West Division of Western Australia (Dampier Archipelago, Barrow Island, and at Millstream on the Fortescue River).

Description. Fore-leg 18-25 (21.5) and hind-leg 27-35 (31.4) % of SVL. Digits slightly compressed; fourth finger a little longer than third. Ear aperture vertically elliptical, $\frac{3}{4}$ - $\frac{3}{4}$ as large as eye. Tail up to 1.8 times as long as SVL, but usually regenerated. Maximum SVL 83 mm.

Nasals widely separate. Prefrontals widely or narrowly separate, rarely touching. Frontals in contact with first two (rarely 3) supraoculars, about as long as combined length of frontoparietals and interparietal. Frontoparietals slightly longer than interparietal. Supraciliaries 6-8 (mostly 7). Upper labials usually 7 with first four wholly or partly anterior to orbit; rarely 6 or 8 with first three or five anterior to orbit; last two largest, usually smaller than lower secondary temporal. Enlarged nuchals 0-3 on each side. Midbody scales in 25-32 rows; dorsals subequal, smooth. Lamellae under fourth toe 19-25, usually divided (especially proximally), weakly to moderately keeled (proximal keels subtubercular, distal keels sharper).

Upper surface pale to moderately dark, dull or glossy, slightly reddish brown. Dorsum covered with dark brown or brownish black spots, variously shaped but seldom circular, less dense and conspicuous than those on flanks and tending to be arranged longitudinally. Flanks pale brown or white, densely covered with dark brown spots, variously shaped, largest and most conspicuous dorsolaterally. Sutures between labials irregularly (but usually broadly) margined with dark brown. Under surface whitish.

Geographic variation. This series falls on the basis of geography and morphology into three groups:

(1) *North-west* (W.A.). Maximum SVL 62 mm. Midbody scale rows 28-32 (mostly 30 and 32). Frontal usually a little longer than fronto-

parietals plus interparietal. Supraciliaries 6-8 (mostly 7). Except on Barrow Island, dorsal and lateral spots tend to be transversely elongate, forming short straight or curved bars; they are especially conspicuous on flanks when ground colour is white, as in the Dampier Archipelago. Dorsal and lateral spots in Barrow Island specimens subcircular, relatively sparse on flanks and aligned longitudinally.

(2) *Kimberley* (W.A.) Maximum SVL 66. Midbody scale rows 25-28 (mostly 28). Supraciliaries 6-8 (mostly 7). Limbs relatively shorter than in other regions. Cockatoo Island specimens are very distinctive with their virtually unspotted backs, darkly margined lower labials, and low number of midbody scale rows (av. 26.5).

(3) *Northern Territory.* Maximum SVL 83. Midbody scale rows 28-31 (mostly 30). Frontal usually a little shorter than frontoparietals plus interparietal. Supraciliaries 7 or 8. Temporals more disparate than in other populations; upper secondary seldom larger than lower.

Remarks. Although the above groups of populations probably represent incipient subspecies, there is too much morphological overlap for their nomenclatorial recognition. In coloration the insular populations are much more distinctive than any from the mainland, but in their meristics they generally agree with the continental populations opposite them; which again creates difficulties in recognising subspecies. Another reason for not at present dividing *i. isolepis* is given under the next subspecies.

Our two topotypes of "forresti" agree well with Kinghorn's description. Nevertheless, few if any of the characters relied on by Kinghorn are exclusive to the Forrest River population.

Material examined. Northern Territory: R 13505-6, 13514 (Yirrkala); R 23266 (26 mi. N of Adelaide River); R 14029, 19891-3, 21917-20, 21922, 21930, 24929 (Katherine); R 23795-6 (Mataranka). Kimberley Division (W.A.): R 11974, 22361 (Kimberley Research Station, Ord River); R 12489-90 (Forrest River Mission); R 11743-7, 11805 (Wotjulum); R 14076, 24996-8 (Cockatoo Island); R 20265-6, 20330, 20352 (Derby); R 1255 (Broome); WHB (5) (La Grange); WHB (1) (Frazier Downs); R 168 (St. George Range). North-West Division (W.A.): R 14017, 14249-51 (Dolphin Island, Dampier Archipelago); R 14359, 14364-5 (Legendre Island, Dampier Archipelago); R 14502 (West Lewis Island, Dampier Archipelago); WHB (2) (Barrow Island); R 5012, 20104-9 (Millstream).

***Sphenomorphus isolepis douglasi* subsp. nov.**

Holotype. R 23446 in Western Australian Museum, collected by G. M. Storr and A. M. Douglas on September 16, 1964, at Darwin, Northern Territory, in 12°25'S, 130°49'E.

Diagnosis. Moderately large and stout *Sphenomorphus* whose adpressed limbs overlap or fail to meet by less than length of fore-leg. Distinguishable from *S. i. isolepis* by its greater

size, fewer upper labials and broad blackish dorsolateral streak on neck and anterior part of body.

Distribution. Far northwest of Northern Territory (east to Oenpelli) and extreme north of Western Australia (Napier Broome Bay).

Description. Fore-leg 17-23 (20.6) and hind-leg 26-35 (31.0) % of SVL. Digits not or very slightly compressed; fourth finger a little longer than third. Ear aperture vertically elliptical or circular, about $\frac{3}{4}$ as large as eye. Tail 1.6-1.8 times as long as SVL. Maximum SVL 96 mm.

Nasals widely separate. Prefrontals widely or narrowly separate, rarely touching. Frontal usually in contact with first two supraoculars, rarely with three, abnormally with one (due to fusion of first and second supraoculars); as long as or a little longer than combined length of frontoparietals and interparietal. Frontoparietals longer or shorter than interparietal. Supraciliaries 6-9. Temporals normally 3; lower secondary usually largest; secondary temporals abnormally divided. Upper labials usually 6 with first three anterior to orbit; occasionally 7 with first four anterior to orbit; last two largest, usually smaller than lower secondary temporal. Enlarged nuchals 0-4 (mostly 1) on each side. Midbody scales in 26-32 rows; dorsals smooth. Lamellae under fourth toe 17-25 (21.4), divided (except distally), weakly keeled (proximally in two series with inner keels apical, larger, subtubercular; and outer keels lateral, sharper; distally smooth or feebly uncarinate).

Upper surface dark glossy brown. Dorsal and lateral spotting varying geographically (see below). Irregular but generally broad blackish dorsolateral streak from neck to a little behind insertion of arm, usually dotted with white and extending narrowly and brokenly through orbit to snout. Under surface whitish, except for grey under digits.

Geographic variation. At present this race is only known from two widely disjunct populations, differing as follows:

(1) *Darwin district (N.T.)*. Maximum SVL 84 mm. Midbody scale rows 27-32 (29.0). Lamellae under fourth toe 18-25 (21.7). Nuchals averaging 1.3 on each side. Supraciliaries 6-8 (6.9). Back sparsely spotted with dark brown. Flanks purplish brown, obscurely flecked with dark brown, sometimes dotted with white (i.e. lateral spotting generally less conspicuous than dorsal).

(2) *Napier Broome Bay (W.A.)*. Maximum SVL 96. Midbody scale rows 26-28 (27.7). Lamellae under fourth toe 17-23 (20.7). Nuchals averaging 0.3 on each side. Supraciliaries 7 or 8 (7.6). Back obscurely mottled (rarely spotted) with dark brown. Flanks pale brown, spotted or mottled with dark brown (i.e. lateral spotting more conspicuous than dorsal).

Remarks.—This distinctive skink is named after Mr A. M. Douglas of the Western Australian Museum, who had a hand in collecting all except three of the type series.

If, as it seems, *douglasi* is confined to humid habitats, the apparent break in its distribution is probably real, for the country round the head

of Joseph Bonaparte Gulf is relatively dry (annual rainfall 25-30 inches). At any rate part of this area (Forrest River and lower Ord River) is now occupied by the nominate race.

I have not formally separated the two segments of *douglasi*, because such a course would mask the fact that they are much more similar to each other than either is to the nominate race. If reasons were found for elevating *douglasi* to a full species, the way would be open for subdividing not only *i. douglasi* but also *i. isolepis* (which as we have seen breaks up into distinguishable populations). One such reason would be the identification of our R 13630 as *isolepis*. This specimen was collected on the same occasion as the Kalumburu paratypes of *douglasi* but differs strikingly from them. It is very pale, lacks the dorsolateral streak, and has relatively shorter limbs, more subdigital lamellae (25), more nuchals (2+1), more upper labials (7), more supraciliaries (9) and more narrowly separated prefrontals than any other Kalumburu specimen.

Paratypes. Northern Territory: R 23447-8 (Darwin); R 23570 (5 mi. E of Darwin); R 23581 (12 mi. E of Darwin); R 23574 (17 mi. E of Darwin); R 23616-23 (Howard Springs); R 23296 (Berry Springs); R 23267-70 (Southport); R 23288-9 (35 mi. SE of Darwin); NTM 1602 (Beatrice Hills); R 13627 (Oenpelli). Kimberley Division (W.A.): R 1567 (Pago); R 13620-5, 13628-9 (Kalumburu).

Sphenomorphus australis (Gray) new combination

Lygosoma australis J. E. Gray, 1839, Ann. Nat. Hist. 2: 232. Australia.

Hinulia gracilipes Steindachner, 1870, S. B. Akad. Wiss. Wien. 62: 342. "Australia, possibly Rockhampton or Cape York."

Diagnosis. Elongate, weak-limbed, thick-tailed *Sphenomorphus* whose adpressed limbs fail to meet by $1\frac{1}{2}$ - $3\frac{1}{2}$ times length of fore-leg. Distinguishable from *S. crassicaudus* by greater size, white spotting of flanks, larger ear aperture and more numerous circumocular scales.

Distribution. Far southwest of Western Australia from Collie south and east to Cheyne Beach.

Description. Fore-leg 10-16 (13.0) and hind-leg 16-27 (21.4) % of SVL. Digits not compressed; fingers extremely short, fourth scarcely longer than third. Ear aperture vertically elliptical, about $\frac{3}{4}$ as large as eye. Maximum SVL 88.5 mm.

Nasals widely separate. Prefrontals moderately separate, rarely touching. Frontal in contact with first two (rarely 3) supraoculars, shorter than combined length of frontoparietals and interparietal. Frontoparietals as long as or a little shorter than interparietal. Supraciliaries 5-7 (usually 6). Temporals 3, upper secondary much the largest. Upper labials normally 7; first three wholly and fourth partly anterior to orbit; last two largest, intermediate in size between primary and lower secondary temporals; third abnormally divided to give 8 labials. Enlarged nuchals 2-4 (mostly 2 and 3) on each

side. Midbody scales in 19-22 (20.5) rows; vertebrals larger than paravertebrals, smooth. Lamellae under fourth toe 16-23 (20.3), smooth, usually entire, occasionally divided (especially proximally).

Upper surface brown (usually dark, slightly rufous brown; occasionally pale olive brown) spotted with black. Spots on head irregular in shape and distribution. Spots on back mostly concentrated on vertebrals to form two broken mid-dorsal lines. Dorsolateral streak ill-defined, black, spotted with white, usually extending narrowly forward to tip of snout and vaguely back on to tail where it tends to become lateral. Sides of body and tail pale olive grey or greyish brown, flecked with black and white. Lips, sides of face and temples whitish, irregularly blotched with black. Lower surface whitish except under tail which is densely mottled with black; throat occasionally marbled with dark grey.

Geographic variation. The Collie specimen is peculiar in several respects. It is darker than any of our 13 specimens from the south coast and is larger (though only 1 mm longer in SVL than R 19834); has fewer midbody scale rows (19 against 20-22); fewer subdigital lamellae (16 against 18-23); and fewer supraciliaries (5 against 6 or 7).

I have not been able to locate the specimen from the mouth of the Murchison referred to by Glauert (1961 : 77).

Remarks. It is unfortunate that there is a prior (but invalid) combination "*Sphenomorphus australis* (Gray)." The latter is based on *Tiliqua australis*, published by Gray on the same occasion as *Lygosoma australis*. When *Tiliqua australis* was transferred by Peters (1863: 231) to *Lygosoma*, it became a secondary homonym of *L. australis* Gray. The next oldest name for *Tiliqua australis*, viz. *Lygosoma lesueurii* Duméril & Bibron (now *Ctenotus lesueurii*), was used in its stead by Boulenger and others until Loveridge (1934 : 345) attempted to revive the dead name *Tiliqua australis* on the invalid grounds that *australis*, though preoccupied in *Lygosoma*, was not so in *Sphenomorphus*. The combination "*Sphenomorphus australis* (Gray) Loveridge," based on a dead name, has no standing in nomenclature and cannot prejudice a similar but later combination based on the available name *Lygosoma australis* Gray.

Nevertheless it was feared that confusion would ensue from proposing the present combination, for Loveridge's combination is well-known and indeed is currently used by some authors. To avoid confusion, the possibility was explored of using *Hinulia gracilipes* Steindachner instead of *Lygosoma australis* Gray on the ground that the latter was indeterminate. Gray's original and subsequent descriptions could apply to several Australian skinks and his type has evidently been destroyed; for, according to Miss E. M. Noble (*in litt.* 6/vii/65), it was not among the specimens salvaged by the British Museum from the neglected collections of the Chatham Museum (*cf.* Sherborn 1940).

However, I was advised not to reject *Lygosoma australis* Gray but to follow Boulenger (1887: 323) in identifying it with the present taxon, because (1) Boulenger's "Catalogue" is still the standard text on Australian skinks, (2) the period of possible confusion would in all probability be short, and (3) the nomenclature of the taxon could be settled once and for all by the simple expedient of designating a neotype. Accordingly I select R 24980 in the Western Australian Museum as the neotype of *Lygosoma australis* Gray; it was collected by Mr R. P. McMillan on January 16, 1965 at Albany, Western Australia, in 35°02'S, 117°53'E.

Material examined. *South-West Division* (W.A.): R 22833 (Collie); R 19834, 24868 (Karri-dale); R 4995-6, 11357, 22473, 24971-3 (Denmark); R 6789, 6791, 24980 (Albany); R 18006 (Cheyne Beach).

Sphenomorphus crassicaudus arnhemicus subsp. nov.

Holotype. R 13513 in Western Australian Museum, collected by Mrs E. V. Mildenhall in 1960 at Yirrkala, Northern Territory, in 12°15'S, 136° 52'E.

Diagnosis. Small, elongate, weak-limbed, thick-tailed *Sphenomorphus* whose adpressed limbs fail to meet by 1-2 times length of fore-leg. Distinguishable from *S. australis* by smaller size and ear aperture, lack of white spots on flanks, and fewer circumocular scales; and from all other races of *S. crassicaudus* by having more than 18 lamellae under fourth toe and frontoparietals never shorter than interparietal. Further distinguishable from *S. c. crassicaudus* (A. Duméril) in lacking sharp upper edge to darkening of flanks, from *S. c. punctulatus* (Peters) by immaculate venter and more numerous nuchals, and from *S. c. darwiniensis* nov. in lacking broad dark vertebral stripe.

Distribution. Extreme northeastern Arnhem Land.

Description. Fore-leg 13-16 (13.9) and hind-leg 20-32 (24.8) % of SVL. Digits feebly compressed; fingers extremely short, never exceeding 2 mm, fourth scarcely larger than third. Tail 1.65 times SVL in single specimen with original tail. Ear aperture slightly sunken, usually circular, 2-4 times as large as nostril, $\frac{1}{2}$ - $\frac{2}{3}$ as large as eye. Maximum SVL 56 mm.

Nasals and prefrontals widely separate. Frontal in contact with first two supraoculars, about as long as combined length of frontoparietals and interparietal. Frontoparietals as long as or a little longer than interparietal. Supraciliaries 5-7 (usually 6). Temporals 3, upper secondary largest. Upper labials usually 7 with first three wholly and fourth partly anterior to orbit; penultimate largest and subequal to lower secondary temporal; occasionally 6 labials owing to fusion of two of first four. Enlarged nuchals 3-5 (mostly 4 and 3) on each side. Midbody scales in 20-22 (mostly 22) rows; vertebrals considerably wider than paravertebrals; smooth. Lamellae under fourth toe 19-22 (20.2), undivided, smooth or tuberculately keeled.

Upper surface glossy, slightly rufous, brown; obscurely dotted with dark brown, most densely on tail. Ground coloration gradually paling on sides, with spots becoming larger, darker and much more conspicuous, especially on lips and sides of tail. Under surface pale except for dark palms and soles and dark brown subcaudal spots which tend to be transversely elongate.

Remarks. The Yirrkala specimen (U.S. Nat. Mus. 128611) identified by Mitchell (1955: 397) as *Lygosoma crassicaudum* Duméril is without doubt an *arnhemicus*. The difference in coloration between this specimen and descriptions of *crassicaudus* (including *ornatus* MacLeay) was pointed out by Mitchell and is confirmed by the present series.

Paratypes. Northern Territory: R 24889-96, 24994-5 (Yirrkala).

Sphenomorphus crassicaudus darwiniensis
subsp. nov.

Holotype. R 23624 in Western Australian Museum collected by G. M. Storr and A. M. Douglas on September 18, 1964, at Howard Springs (15 air-miles east of Darwin), Northern Territory, in 12°28'S, 131°03'E.

Diagnosis. Small, elongate, weak-limbed, thick-tailed *Sphenomorphus* whose adpressed limbs fail to meet by 1-2 times length of fore-leg. Distinguishable from *S. australis* and other races of *S. crassicaudus* by broad dark vertebral stripe separated from dark flanks by broad pale paravertebral stripe. Further distinguishable from *S. crassicaudus arnhemicus* by having fewer than 18 lamellae under fourth toe and frontoparietals never longer than interparietal.

Distribution. Far northwest of Northern Territory (south to Adelaide River) and extreme north of Western Australia (Napier Broome Bay).

Description. Fore-leg 12-15 (13.8) and hind-leg 19-27 (24.0) % of SVL. Digits feebly compressed; fingers extremely short, fourth scarcely longer than third. Ear aperture slightly sunken, circular or vertically elliptical, 2-3 times as large as nostril, $\frac{2}{3}$ - $\frac{3}{4}$ as large as eye. Tail 1.5 times as long as SVL in single specimen with original tail. Maximum SVL 58 mm.

Nasals widely separate. Prefrontals widely or narrowly separate. Frontal in contact with first two supraoculars, about as long as combined length of frontoparietals and interparietal. Frontoparietals slightly shorter than interparietal. Supraciliaries 5 or 6 (usually 6). Temporals 3, upper secondary much the largest. Upper labials 7 with first three wholly and fourth partly anterior to orbit, last two subequal largest and intermediate in size between primary and lower secondary temporals. Enlarged nuchals 3 or 4 on each side. Midbody scales in 20 rows, except for one specimen with 21; vertebrals considerably wider than paravertebrals; smooth. Lamellae under fourth toe 15-17 (15.8), undivided, tuberculately keeled.

Top and sides of head uniformly dark glossy brown. Broad dark-brown vertebral stripe covering inner $\frac{3}{4}$ of vertebral scales, tending

anteriorly to be split into two stripes by pale mid-dorsal line. Broad pale-brown paravertebral stripe covering whole of paravertebral scales and outer quarter of vertebrals. Sides of body and tail greyish brown flecked with dark and pale brown, dark dots concentrating superiorly to form dark but indistinct dorso-lateral line. Lips whitish, sutures between labials broadly edged with dark brown. Under surface whitish, except for dark palms, soles and under digits, and sparse dots under tail.

Remarks. The widely disjunct range of this taxon is similar to that of *S. isolepis douglasi*. I know of no parallel in other animals. Birds restricted in Western Australia to the vicinity of Napier Broome Bay are generally distributed in the Northern Territory more widely than these lizards. The owl, *Ninox rufa rufa* (cf. Mees 1964 : 8) may prove exceptional; when unconfirmed sight records are ignored, its known range is much the same as that of *darwiniensis* and *douglasi*.

I have been unable to find the Ord River specimens on which Glauert (1961 : 61) based the inclusion of "*Lygosoma* (*Omolepida*) *punctulatum*" in the fauna of Western Australia. The only specimen so labelled was our *darwiniensis* from Pago.

Paratypes. Northern Territory: R 21975 (Darwin); R 24000 (Snake Creek, 7 mi. N of Adelaide River). Kimberley Division (W.A.): R 955 ("Drysdale River" = Pago, Napier Broome Bay).

Discussion

In his classification of the lygosoma skinks Boulenger was less concerned with the establishment of natural groups than with the identification of species; hence the reliance in his keys on a few good "pigeon-holing" characters. One measure of his success is that since the publication of the 'Catalogue' few names have been inadvertently proposed for taxa already described. The obverse side of his work is the instability in nomenclature resulting from the prevailing reluctance of workers to accept his generic classification, especially the extremely broad concept of *Lygosoma*.

Boulenger's subgenera of *Lygosoma* have been variously raised to full genera; but as Malcolm Smith showed, this leads to conceptual difficulties, for Boulenger's subgenera were merely intended as means to identifying species and provide no basis for a natural classification. Smith therefore took the opposite (and logical) course of reducing some of the subgenera to sections and abandoning others altogether. He evidently did not think it possible to divide *Lygosoma* into natural, convenient-sized units, a task that Mittleman courageously undertook.

Mittleman's classification was evidently based on descriptions of species rather than the animals themselves. His choice of characters was thus limited to those mentioned in Boulenger's somewhat meagre accounts. Moreover the characters were not analysed for taxonomic constancy or for phylogenetic significance. Consequently several of his numerous genera, despite

their small size, are not clearly monophyletic. As for the very large genus *Sphenomorphus*, Mittleman himself conceded that it might be composite.

While I am confident that all the Western Australian and Northern Territory species are congeneric. I am not so certain that they are rightly placed in *Sphenomorphus*. In spite of their different habitus, these species are all very similar in scutation, especially of the loreal and circumocular regions, in which respect they are less like the type of *Sphenomorphus* than are the species segregated by Smith and Mittleman in *Otosaurus*. It may therefore prove necessary to revive *Eulamprus* or *Hinulia* for the Australian "Sphenomorphus" and their Papuan relatives.

Apart from generic uncertainty, the trivial names of the Australian species cannot be regarded as final until revision of the numerous eastern forms (begun by Copland 1945) is complete. Nor can my treatment of the western forms be regarded as final. It is still an open question whether *douglasi* and *isolepis* are conspecific, and whether either of them should be subdivided. In the series *richardsoni-fasciatus-pallidus*, I have drawn the specific boundary between the first two; it may prove to be better placed between the last two.

Acknowledgements

I am grateful to Miss E. M. Noble (Reptile Section, British Museum) for information on the type of *Lygosoma australis* Gray; to Mrs A. Neumann (Librarian, Western Australian Museum) for translating papers from German; to Dr. W. D. L. Ride (Western Australian Museum) for nomenclatorial advice; and to Messrs K. R. Slater (Northern Territory Administration) and F. J. Mitchell (South Australian Museum) for the loan of specimens in their care.

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3.—Cretaceous dinosaur footprints from Western Australia

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Abstract

Footprints and trackways long known to be exposed in the Lower Cretaceous Broome Sandstone near Broome, Western Australia have been re-examined, and are here attributed to a theropod dinosaur, designated as *Megalosauropus broomensis*, gen. & sp. nov.

Introduction

A preliminary account of the occurrence of large footprints in the Broome Sandstone, of early Cretaceous age, near Gantheaume Point, Broome, West Australia (17° 59'S, 122° 11'E), was published by Glauert in 1952. This account appears to have been based upon reports and measurements, together with a cement cast of one of the prints made by residents of Broome, and not on Glauert's own observations in the field. He attributed the prints to "dinosaurs". Subsequently McWhae *et al* (1958) in their description of the Broome Sandstone, identified the prints more specifically as iguanodont tracks, but gave no reason for this identification.

We visited the exposure on May 25th and 26th 1964 and obtained casts of four of the best preserved footprints, three at Gantheaume Point and one near Riddell Beach. The following report is based on this visit, on a subsequent visit by one of us (D.M.) to the site in August 1964, and on supplementary measurements and checks kindly made for us by Messrs. J. Tapper and M. Gower of Broome.

At this place we wish to express our deep appreciation not only for the assistance mentioned above, but also for much help given us by Mr. Tapper and his brother, M. Edgar Tapper as well as by Mr. Edgar Truslove of the MacRobertson Miller Airlines, in making casts of the footprints, in packing them for shipment, and in the supervision of their transport from Broome to Perth.

Before presenting a description of the tracks and trackways that form the subject of this paper a few remarks will be inserted, to explain our reasons for employing a Linnaean name. In doing this we have been influenced by Peabody (1940 and 1955) and by Baird (1957). As these authors have shown, if designations that clearly indicate the nature of the fossils as tracks and trackways are used, and if the fossils are properly described and interpreted according

to the best modern knowledge of such objects, there is every valid reason for giving formal names to them according to the Linnaean system.

"I submit that the characters most diagnostic for the classification of footprints as such, as well as most useful for comparison with skeletal remains, are those which reflect the boney structure of the foot. In most adequately known varieties of dinosaur footprints the presence of articular swellings and pads permits a reasonably accurate analysis of the skeletal pattern." (Baird 1957 p.469).

The tracks and trackways at Broome fulfil the requirements specified by Peabody and by Baird as necessary for the proper study and interpretation of fossils of this nature.

Location

Several groups of footprints were observed. One group in rocks exposed near the north-western end of Riddell Beach consisted of two clearly-defined and one ill-defined print. The second group comprised 10 prints, mostly well-defined, about 150 feet seaward of cliffs near the lighthouse at Gantheaume Point. The third group comprised about 10 ill-defined prints about 200 feet seaward of the same cliffs. The geographical distribution of prints of the second group is shown in Figure 1. Print numbers in Figure 1 represent a field system, later shown to be untenable; they may now be taken as arbitrary numbers.

All three groups are normally covered by sea water and are easily accessible only at very low tides. The more seaward group at Gantheaume Point is exposed only at tides of +1.9 feet or less above the arbitrary datum from which Broome tides are estimated for the North and Northwest Tide Table published by the Harbour and Light Department of Western Australia. The more landward group at Gantheaume Point is accessible below +2.9 feet. The Riddell Beach group is a little higher.

The Broome Sandstone

McWhae *et al* (1958) describe the Broome Sandstone as variegated micaceous sandstones often strongly crossbedded, with subordinate siltstone. A thickness of at least 900 feet has been recorded in bores near Broome, but only about 40 feet are exposed in the type section at Gantheaume Point. The Broome Sandstone is known to lie on the Jarlemai Siltstone, which contains both macro- and micro-fossils of Upper Jurassic age. South of Broome the Broome Sandstone is overlain disconformably by the Parda Formation, from which fossils have not

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DINOSAUR FOOTPRINTS near GANTHEAUME POINT, BROOME, WESTERN AUSTRALIA

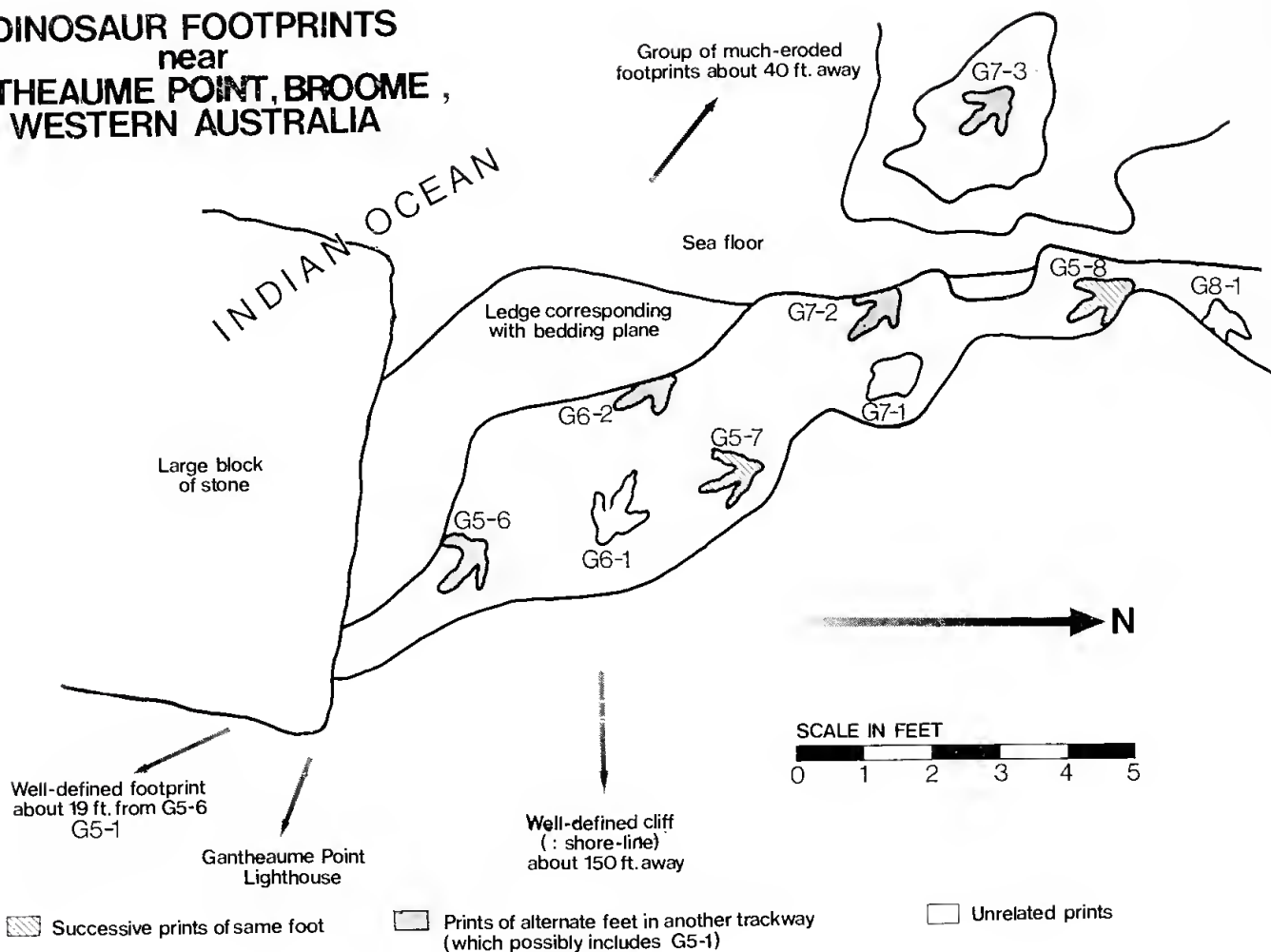


Figure 1

been recorded. McWhae *et al* (1958) tentatively assign both the Parda Formation and (because of "Lower Cretaceous affinities" of the fossil plants contained in it) the Broome Sandstone, to the Lower Cretaceous, possibly the Neocomian.

We found ripple marking, with wave lengths varying from two or three to ten or twelve centimetres, to be characteristic of the Broome Sandstone, which appeared to be quite or nearly horizontally bedded. Presumably each of the three sets of footprints noted above, exposed at different levels, was made at a different time, separated by an interval the duration of which we cannot estimate at present.

Description and Discussion of the Tracks

Megalosauropus, gen. nov.

Diagnosis. Bipedal trackway, with pace angulation about 140°-160°, stride about 2 meters at a normal walk. Individual impressions large (order of 325 millimetres in length), three-toed, and with the angulation of the digits showing an average of about 35° to 45°. Each impression showing second, third and fourth digits with phalangeal formulae of 3 for digit II, 4 for digit III and 5 for digit IV. Trackways probably those of a megalosaurian carnosaur.

Type. *Megalosauropus broomensis*, sp. nov.

Megalosauropus broomensis, sp. nov.

Holotype. Western Australian Museum No. 662,51 (fibreglass mould of print G 5-6).

Paratypes. Western Australian Museum, Nos. 64.6.5 and 64.6.7 (plaster casts of footprints G 5-7 and G 6-1 respectively).

Topotypes. Numerous footprints and trackways in place, at the type locality.

Horizon. Broome Sandstone, of Lower Cretaceous affinities.

Locality. Gantheaume Point, near Broome, Western Australia.

Diagnosis. As given for the genus, above.

Three groups of prints were seen near Broome, and casts were obtained from two of these groups. For the purposes of this present description and discussion, however, only those three casts obtained from the more landward set of trackways at Gantheaume Point, plus studies and photographs of the trackways in situ, are used. The more seaward set of trackways, evidently the ones described by Glauert, were far too battered by wave action to be of any real value for this study. The few prints seen at Riddell Beach, from which one cast was made, did not preserve enough details for effective study. Our study is based on one set of closely associated track ways, all made at one time, since all are exposed at the same topographic and stratigraphic level.

It is evident that the trackways at Gantheaume Point represent one kind of animal, and in all probability a single species. Moreover, these prints appear to be, because of close correspondence in size and structure, conspecific with

the prints at Riddell Beach, even though the latter are separated from the former by a horizontal distance of several hundred yards and a vertical stratigraphic separation of several feet.

The cast of one of the prints, (G5-6) shows very clearly the articular swellings and pads which in turn reveal the structure of the foot, so the description is based primarily upon it, supplemented by information from the other two casts. G5-6 is approximately 325 mm. (about 13") in length. The middle of the three toes is the longest, and the somewhat shorter side toes diverge from it at angles of about 35° to 40°. The print indicates a very bird-like foot, with slender toes terminating in sharp claws, and with no webbing between the toes. (It seems reasonable to think that if there had been any strong webs between the toes, such would have been evident in the prints, considering the fine details shown in the impressions of the toes themselves).

The middle digit of G5-6 shows very clearly the articular swellings between four phalanges. These indicate the first phalanx to be longer than the second, the second longer than the third, and the third longer than the fourth. An imprint of the tip of the claw is shown. There is a large "heel print" shown in this track, as in the other footprints from Broome, made by the downward pressure exerted by the third metatarsal at its junction with the proximal phalanx of the third digit. The junctions between the second and the fourth metatarsals and their contiguous phalanges are not recorded in the print, since the distal ends of these shorter metatarsals were elevated to such a degree that they did not come in contact with the ground, even during the implantation phase of the stride, when there was the greatest con-

tact between the foot and the substratum. However, the articular swellings between the first and second phalanges of both the second and fourth digits are clearly indicated. In G5-6 the distal phalanx of the second digit is large, and it is known from numerous fossils of carnosaurian pedes that the claw of the second digit is much the largest of the three claws.

Thus in all respects the details of an individual print of *Megalosauropus* can be correlated point by point with the boney structure of a large carnosaurian pes, particularly of the foot in such genera as *Megalosaurus* itself and *Antrodemus*. It should be added that there is a reasonably close correspondence in size between the footprints here described and the pedes of the two genera mentioned immediately above.

Since certain aspects of foot structure are so well shown in the prints from Gantheaume Point, an attempt is made to indicate the proportions of various phalanges, these being based upon measurements of the casts. In general measurements have been taken at the approximate mid-portions of the articular swellings and pads, these being considered as usually indicative of the joints between phalanges. Peabody (1948 p.402) would place the joints between the ultimate and penultimate phalanges as about coincident with the posterior end of the most distal swelling, a detail with which Baird (1957 pp.456-461) does not agree. Baird would enclose both ends of the fourth phalanx of digit IV within the distal pad. Following Baird's interpretation for the relationships between articular swellings and pads and the boney structure of the foot, and making direct comparisons of these footprints with the bony structure of the foot in *Antrodemus* (because it is available, and closely related to the form under consideration) results have been obtained as shown in the accompanying Table 1.

TABLE 1

Comparisons of foot dimensions in *Megalosauropus* and *Antrodemus*.

<i>Megalosauropus</i> (Broome G5-6) Length of phalanges derived from measurements between digital swellings and pads of footprints Lengths (mm.)	<i>Antrodemus</i> A.M.N.H. 5753 Measurements along ventral surfaces of phalanges Lengths (mm.)
Digit II	
Phalanx 1 —	118
2 50	83
3 55 (110% of phalanx 2)	101 (122% of phalanx 2)
Digit III	
Phalanx 1 100	134
2 60 (60% of phalanx 1)	89 (66% of phalanx 1)
3 56 (56% of phalanx 1)	71 (53% of phalanx 1)
4 46 (46% of phalanx 1)	66 (49% of phalanx 1)
Digit IV	
Phalanx 1 —	90
2 55	65
3 40 (73% of phalanx 2)	43 (66% of phalanx 2)
4 28 (51% of phalanx 2)	36 (55% of phalanx 2)
5 23 (42% of phalanx 2)	62 (95% of phalanx 2)
Length of footprints including Metatarsal III pad —325	Length of Digit III phalanges + Metatarsal III articulation —435

TABLE 2

Comparison of trackway characteristics in *Megalosauropus* (Broome, W.A.) with those of an unnamed carnosaur from Glen Rose, Texas, U.S.A.

	<i>Megalosauropus</i>	Glen Rose, Texas
Stride (mm.)	2048 1843	3150 3090 3120
	av. 1946 (approx. 6'4")	av. 3120 (approx. 10'3")
Pace (mm.)	1126	1610 1540 1550 1570
	av. 1065 (approx. 3'8")	av. 1567 (approx. 5'2")
Pace Angulation	160° 140°	149° 152° 163°
Interpes distance		Essentially 0 (The tips on the inner toes are normally on the mid-line)
Angulation of digits	35° — 45°	37°

Four prints at Gantheaume Point in the more landward exposure form a trackway, these being the prints G7-3, G7-2, G6-2 and G5-6 (see Figure 1). In addition, G5-8 and G5-7 appear to be successive prints of the same foot in another trackway. The first of these two trackways is oriented about N 140°, the second about N 155°.

The figure published by Glauert, (1952) showing the more seaward group of tracks at Gantheaume Point, indicates two trackways, more or less parallel to each other and both oriented in the same direction, toward the south. It is interesting that the two trackways in the landward set, mentioned above, are also directed in a generally southerly direction. The four prints, G7-3, G7-2, G6-2 and G5-6 show a pace of more than 1 metre (about 3' 6" to 3' 8") and a stride (6' 8") of about 2 metres. This may be compared (see Table 2) with a trackway made up of five prints from the Lower Cretaceous Glen Rose Formation of Texas, now on display in the Brontosaurus Hall of The American Museum of Natural History. In the Glen Rose trackway the strides ranges between 3.09 metres (about 10' 2") and 3.15 metres (about 10' 4"). The Texas prints are larger than those at Gantheaume Point, so the difference between the stride in the two dinosaurs is not surprising. The ratio of track length to stride is remarkably similar in the two sets of trackways, as shown below (all dimensions in millimetres):—

	Gantheaume Point, W.A.	Glen Rose, Texas
Length of print	325 (G5-6)	a. 500 (smallest) b. 520 (largest)
Length of stride	2048	c. 3090 (shortest) d. 3150 (longest)
Ratio		
Length of print/ Length of stride	16%	(a/d) 16% (b/c) 17%

The Gantheaume Point trackways show that the feet were oriented in fore and aft fashion; that is, the axis of the middle toe is more or less in line with the direction of the stride. The same is true for the Glen Rose trackway. There was generally no twisting of the foot while walking in these large carnosaurian dinosaurs; rather they walked in a very bird-like fashion, as is certainly to be expected from their great weight. Any marked twisting of the foot during locomotion would have been not only inefficient but also dangerous for animals of this size. In this respect one may compare them with heavy mammals of the present time, such as horses or rhinoceroses or elephants, in which the foot is constructed for rectilinear action during locomotion.

Moreover, the *Megalosauropus* trackways show, as does the Glen Rose trackway, that these giant carnososaurs swung the leg antero-posteriorly, bringing the foot down close to the mid-line, again as might be expected in animals of such great weight. This would have maintained the feet directly beneath the body and in line with the centre of gravity. Thus the inner toes of the right and left feet commonly meet the midline in these trackways and the pace angulation is wide, being 140°-160° in the Gantheaume Point trackway and 149°-163° in the Glen Rose trackway.

Particular attention has been given in the foregoing discussion to a comparison of the prints and trackways of *Megalosauropus*, found in the Broome Sandstone, with the prints and trackway of the as yet unnamed carnosaurian dinosaur from the Lower Cretaceous Glen Rose formation of Texas. It has been shown that close resemblances exist between the impressions made by large predatory dinosaurs that were living on opposite sides of the world during early Cretaceous time. Moreover, these resemblances are one indication of the wide distribution of the large theropod dinosaurs, during early Cretaceous history, and by inference of the various gigantic herbivorous dinosaurs upon which they fed.

In addition to the trackways described above, there are some other prints and trackways that give additional information as to the distribution of the carnosaurs during the early phases of Cretaceous history. Of particular importance are the trackways described by Sternberg (1932) from the Lower Cretaceous sediments along the Peace River, British Columbia. Several hundred footprints, many of them associated in trackways, were found at this locality, representing, according to Sternberg's description, some six genera. Although Sternberg did not attempt to assign the prints he described to categories larger than the genus, it is quite evident that one type, namely *Irenesauripus mclearni*, in which the length of the individual footprint is 380 mm. and the average stride is 940 mm. is rather close to *Megalosauropus* in size, while *Irenesauripus occidentalis*, with a footprint length of 500 mm. and "stride" (really pace) stated to be about 1000 mm. may be compared with the tracks from Glen Rose, Texas (Sternberg 1932 p.62 cf. p. 65).

Mention should be made also of the many imprints found in Lower Cretaceous near-shore deposits in Georgia, U.S.S.R., and described by Gabounia (1951). One genus (*Satapliasaurus*) would seem to represent a theropod somewhat smaller than *Megalosauropus*, since its prints (assigned by Gabounia to three different species) show a range of print length from 220 to 250 mm. and of a stride from 600 to 700 mm.

It seems obvious that megalosaurian carnosaurs were even more widely distributed than these several records indicate. The bones and prints of Lower Cretaceous iguanodonts have been found at many localities in Europe, in central Asia, in North America, in South Africa, in the island of Spitzbergen, and in Australia. By an inference opposite to the one made three paragraphs above, it may be supposed that where these large herbivores wandered there would also be predators, in other words megalosaurs, to feed upon them. All of this points up the fact that there were continental connections permitting the large dinosaurs to migrate widely throughout the world during Middle and Late Mesozoic times. The presence of *Megalosauropus* in Western Australia makes one more link in the chain of evidence as to the distribution of these interesting reptiles at the time of their dominance.

Conclusions

From the foregoing description it can be seen that *Megalosauropus*, as known from trackways exposed at Gantheaume Point, near Broome, Western Australia, is a large carnosaurian dinosaur with most of the attributes in the individual footprints and in the trackways that are to be expected in such an animal. Since the Broome Sandstone is now regarded as of early Cretaceous age, being placed well down in the Neocomian (see McWhae *et al*,

1958) these trackways may be regarded as representative of a large megalosaur, perhaps even of *Megalosaurus* itself. But since these are only the trackways they have been given a separate designation, for the reasons discussed by Peabody (1940 and 1955) and Baird (1957). They indicate a dinosaur similar to the one (as yet unnamed) that made the Glen Rose trackway, this latter being somewhat later (of Aptian age) than the one in the Broome Sandstone. Finally, the trackways of *Megalosauropus broomensis* give valuable new evidence as to the world-wide spread of the carnosaurian dinosaurs in early Cretaceous time.

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In the preparation of references, and for all matters of presentation not otherwise covered in these instructions, authors are required to follow the C.S.I.R.O. *Guide to Authors* (Melbourne, 1963). Failure to read through this carefully before preparing papers may lead to delay in publication. The use of the various conventional systems of nomenclature recommended in this booklet, and in the supplementary pamphlets referred to in it, is obligatory; for this purpose, palaeontological papers must follow the appropriate recommendations for zoology or botany. All new stratigraphic names must have been previously approved by the Stratigraphic Nomenclature Committee of the Geological Society of Australia.

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Authors are solely responsible for the accuracy of all information in their papers, and for any opinion they express.

**Journal
of the
Royal Society of Western Australia**

Volume 50

1967

Part 1

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Membership list of the Society, 1966-67.

Editor: A. F. Trendall

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The Royal Society of Western Australia, Western Australian Museum, Perth

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Part 2

4.—The mineral resources of Western Australia and their potential

Presidential Address, 1966

by J. H. Lord*

Delivered 18 July 1966

Abstract

The history of mineral production over the past 124 years is outlined, and the present development and the potential of the more important minerals such as iron, petroleum, bauxite, gold and nickel is discussed. The value of mineral production should increase from the present \$A53 to \$A245 million per year during the next five years, while intensive prospecting may locate new major deposits of such minerals as copper, lead, nickel, potassium salts and phosphates.

Introduction

Like many other States and countries, the development of Western Australia can be linked closely with the development of the State's mineral resources. Until 1953 gold was by far the most important mineral produced and the total mineral production was largely a reflection of the value of gold won. Coal was the only other mineral mined continuously over this period.

Although some copper was mined near Northampton in 1842, by 1872 the Government of the colony, realising that a gold strike was required to stimulate progress, offered a reward of £5,000 to the discoverer of a field which could produce 10,000 ounces of gold.

In 1885, the Government financed a prospecting venture under the leadership of Hall to examine in detail a portion of the Kimberley area, where in the previous year Government Geologist E. T. Hardman had found reef and alluvial shows of gold. Three years earlier another prospector named Saunders claimed to have found a trace of gold in this area while travelling through to the Northern Territory. Payable gold was discovered on the 14th July, 1885, and by 1886 over 2,000 people were prospecting in the area. The find did not prove as rich as expected and the reported production did not reach the required 10,000 ounces, although the target may have been reached if all of the gold had been sold through the correct channels. An inquiry by a select committee of the Government recommended £500 reward to Hall's party and £500 to Geologist Hardman.

Disappointed in the Kimberley area, the prospectors from other States and overseas drifted southwards, where gold discoveries followed in quick succession in the Pilbara, Murchison, and Yilgarn, and in 1892 Coolgardie was discovered, followed by Kalgoorlie in 1893.

With the location of the fabulous "Golden Mile" at the latter centre, the population of the State showed its period of greatest growth when it almost quadrupled from 48,502 to 179,967 in the last decade of the century.

Many of the very rich finds were quickly worked out but others persisted and became established mines. On the total mineral production chart (Fig. 2) or on the gold section of Fig. 3, it can be seen that gold reached production peak in 1903 and then began to decline steadily. This decline was hastened during World War I and in the following years.

The disappointed prospectors did not leave the State but turned to other occupations, in particular wheat and wool production. While gold declined, these primary industries developed because of the additional manpower and finance brought to the State, as shown in Fig. 2.

When these new industries suffered from the depression in the 1930's, there was a return to the goldfields, and when the price of gold increased, gold production again rose and helped considerably to cushion the effect of the depression in this State. The rise was again turned to a slump by World War II, but although an upward trend developed on the cessation of hostilities, this recovery was handicapped by the fixed price of gold. For some years, however, the mining engineers managed to overcome this by improved efficiency and techniques, but these methods could not continue to offset the steeply rising wages and costs. By 1953 the production of gold reached the peak of its post-war recovery, remained static for a few years and is now declining (see Fig. 3). This decline must continue unless there is a substantial rise in the price of gold.

About 1953 mining companies began to realize that, even if new gold finds were made, the economic situation precluded their development unless the grade of ore was very high. Gradually therefore, the companies became interested in "minerals other than gold". The interest in these minerals began to increase due to the expanded production of asbestos, iron and manganese and, later, the development of mineral sands in the south-west and bauxite in the Darling Range. In 1964 the production exceeded the value of gold produced for the first time.

It may be asked why these minerals were not developed earlier. There were no doubt many reasons but, in my opinion, the more important ones were that prospectors and mining com-

* Director, Geological Survey of Western Australia, Perth.

MAP OF WESTERN AUSTRALIA

Showing mineral localities and geology

SCALE OF MILES
40 0 40 80 120 160 200

Precambrian areas
Sedimentary basins
Continental shelf

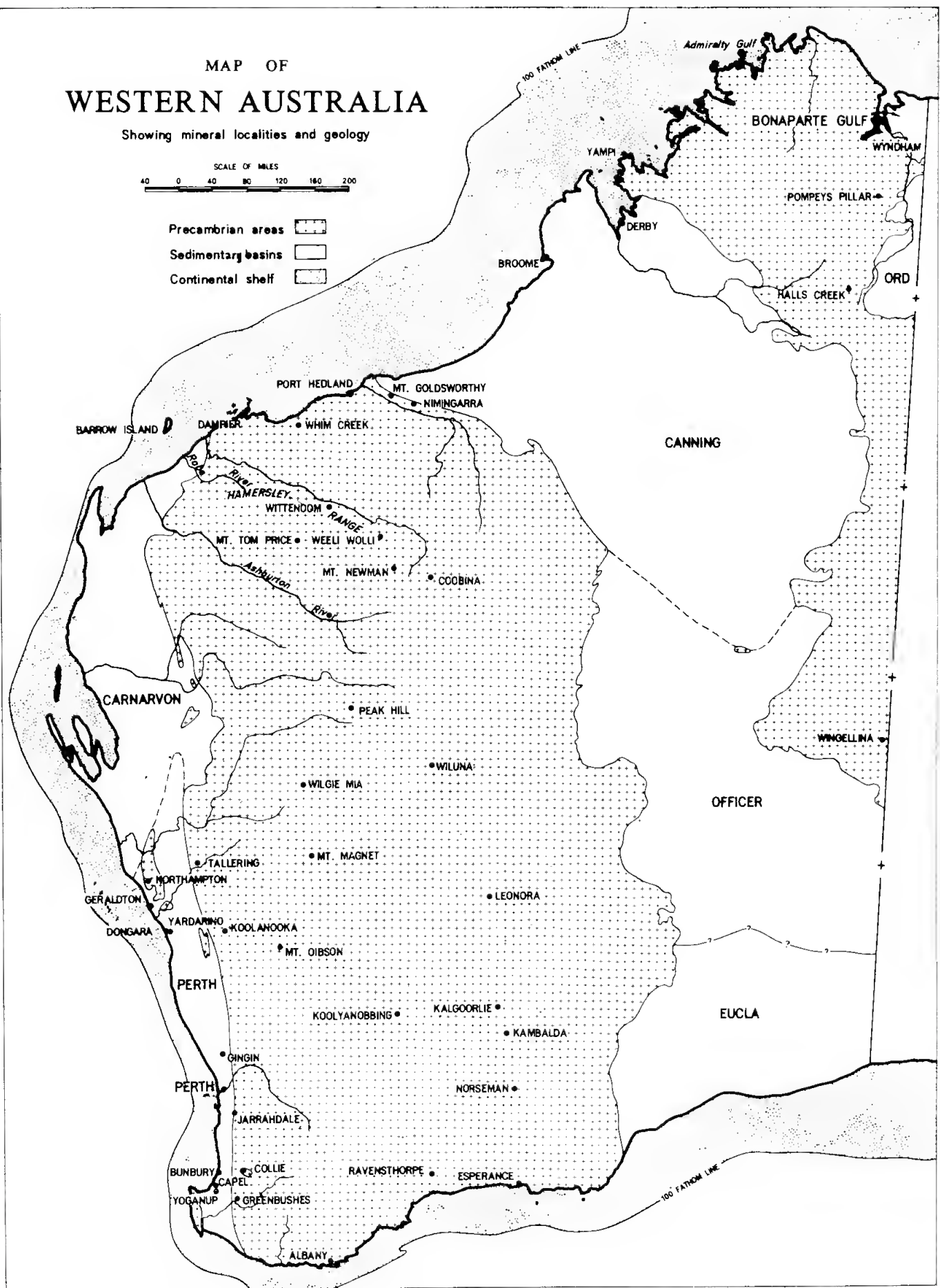


Fig. 1.—Western Australia showing some mineral localities and regional divisions.

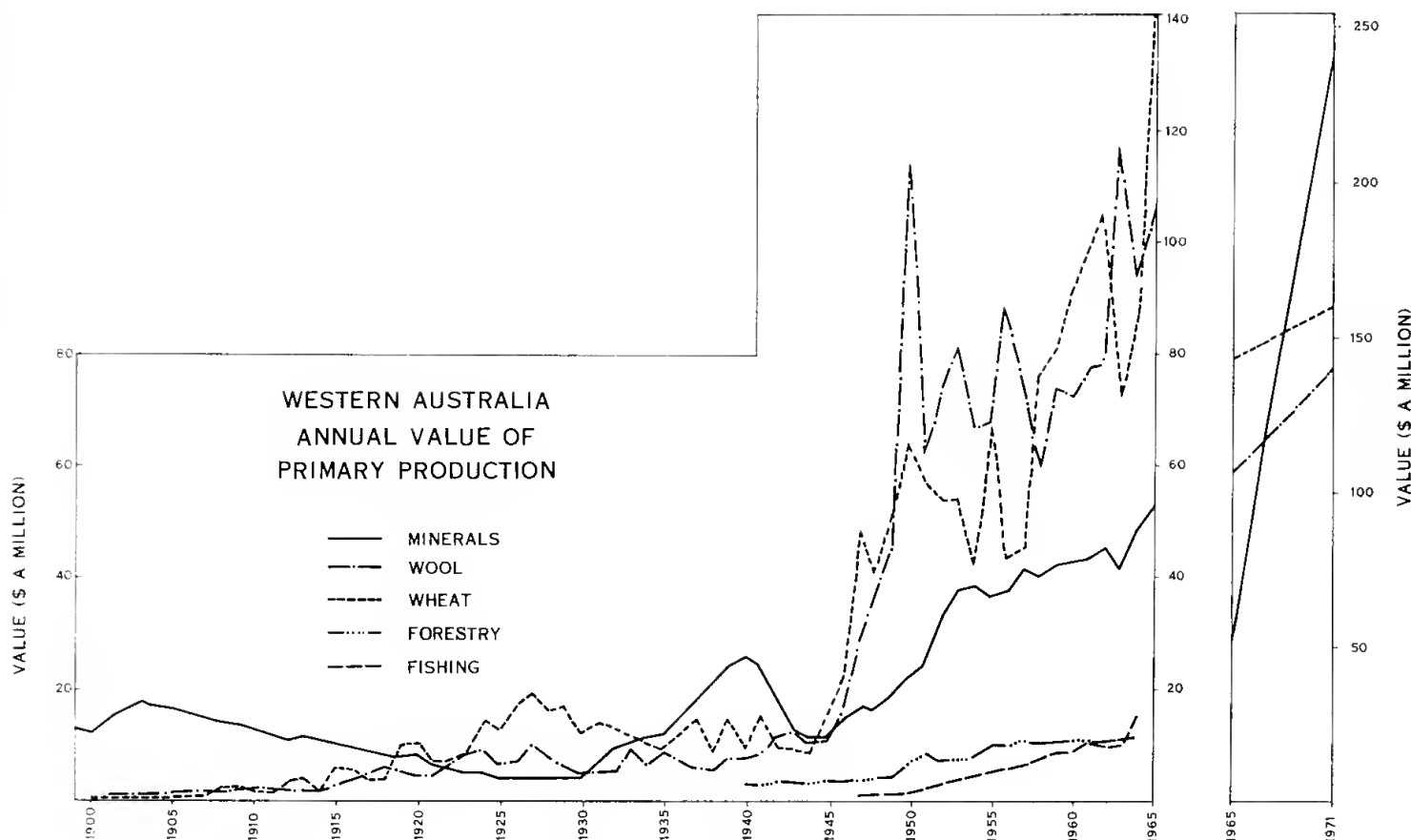


Fig. 2.—Annual Value of Primary Production, Western Australia, 1899 to 1965 and projection to 1971.

panies were too fascinated with the get-rich-quick prospects of gold, and that there was a lack of capital and developed overseas markets for other minerals. The prospector has been interested always in gold, as it is easy to identify and easy to estimate the grade of a find by panning. A rich alluvial patch offers quick rewards, or, if in reefs, it is easy to treat as the Government provides treatment facilities.

The age of the prospector is passing, as the opportunities for quicker rewards from gold are now rare and prospecting for minerals other than gold is more difficult from all aspects. Full credit and recognition must be given to the early prospector who penetrated the isolated areas of this State in his search for gold. Originally the company would wait for the prospector to make a find and then purchase it from him, but nowadays companies are being forced to do their own prospecting. This has resulted in the geologist becoming the modern prospector in the search for surface and concealed ore bodies, using aids which are far beyond the scope or comprehension of the original prospector.

Oil exploration is carried out on a highly scientific basis with the extensive use of geophysics and has led the way in this State with the application of new techniques for prospecting.

Exploration for other minerals in this State is following this lead and now companies are using the latest airborne and surface geophysical techniques and geochemical methods to assist the geologist to unravel the sub-surface structures. These methods are costly to operate and account for the millions of dollars being spent

on mineral search. The reward is the increase in the State's total mineral production (see Figs. 2 & 3), since 1952 and the great increase expected within the next few years.

The bauxite in the Darling Range is an example of how new mineral deposits are found or developed. For many years it was known that bauxite occurred here but it was never investigated thoroughly until one company decided to take the risk. It spent thousands of dollars on basic geological studies, detailed sampling, drilling and the establishment of a special laboratory for assaying. Finally, when the bauxite was thought to be present in significant quantity and grade, detailed investigations of the metallurgical problems associated with the treatment of the ore were carried out. The result is the thriving alumina industry at Kwinana.

Before discussing minerals in detail, I should like to mention one mineral which is not shown on any production table, nor is its value reported anywhere in dollars. It is water, which is far more important to this State than any other mineral mentioned below. Its potential is limited and it requires careful conservation to ensure that all the State's future requirements are met. The Government is conscious of this fact and has eleven geologists engaged on the search and evaluation of ground water supplies, which is equivalent to the complete strength of the Geological Survey 5 years ago.

There are many ways of classifying mineral occurrences geologically, but for this general discussion they are considered in three regional groups: firstly, those which occur on or associated with Precambrian rocks; secondly, those which occur associated with sedimentary basins

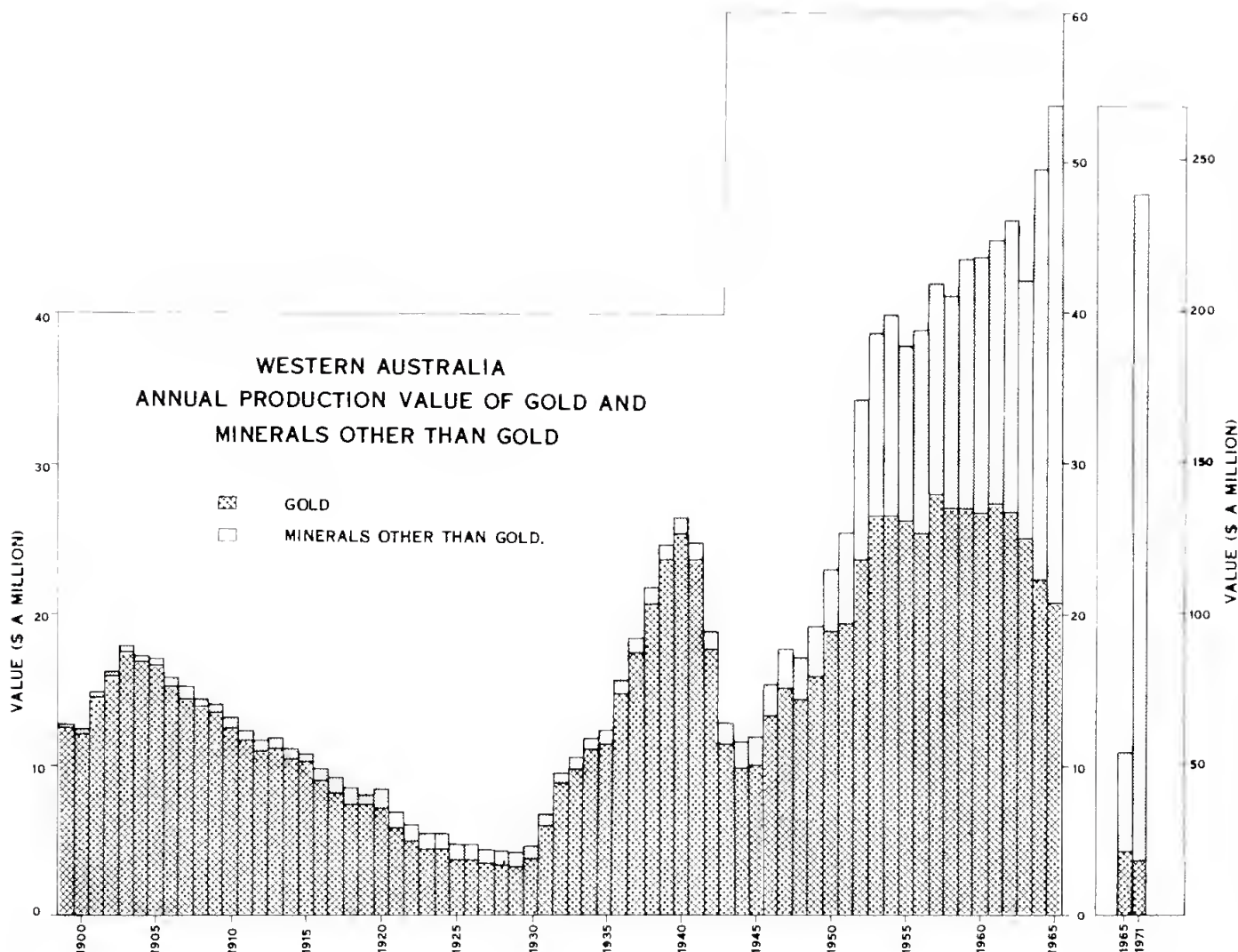


Fig. 3.—Annual Production Value of Gold and "Minerals other than Gold", Western Australia, 1899-1965 and projection to 1971.

and thirdly, those which may occur offshore on the continental shelf. These regional divisions are shown on Fig. 1. Only minerals which are or will be produced on a substantial scale are considered.

Precambrian region

The Precambrian rocks cover an area of over 600,000 square miles or nearly two-thirds of Western Australia (see Fig. 1). The age of rocks covers the full span of the Precambrian from 600 million to over 3,000 million years. Some have been altered physically and chemically many times; others, such as the Brockman Iron Formation, are relatively unaltered, while all have undergone surface erosion over a very long period.

Gold.—Archaean basic lavas, basic and acid intrusives, metasediments and banded iron formation have acted as hosts for gold mineralization, which is estimated to have occurred 2,300 million to 2,400 million years ago. The semi-arid climate and erosion over a long period of geological time have favoured surface enrichment of deposits, while for similar reasons alluvial deposits are rare.

The State has produced 65,538,978 ounces of gold valued at \$A1,009,686,910. Kalgoorlie has produced 36,094,574 ounces while Leonora,

Norseman, Wiluna, Mt. Magnet and Day Dawn are centres each of which have produced over 1 million fine ounces.

Potential.—The history of the gold industry has been outlined earlier and unless there is a substantial increase in the price of gold, production will continue to decline.

The amount of prospecting already done, indicates that the chances of finding new high-grade deposits at the surface are not favourable. Any large new mines would be on large low grade ore bodies or on concealed ore bodies.

Bauxite.—The aluminous nature of the Western Australian laterites has been known for many years, but their commercial value was not appreciated until Western Mining Corporation carried out an expensive detailed investigation in the Darling Range.

The bauxite, consisting of hydrated oxides of alumina and iron with silica in varying proportions, occurs in the lateritic profile. It contains from 30 to 45 per cent alumina, with silica and iron as the main impurities. The silica is in the form of unreactive quartz and does not create refining problems.

Another occurrence of bauxite has been reported from the North Kimberley near Admiralty Gulf. The occurrence is the text book

example of bauxite in the laterite profile over the Carson Volcanics. The deposit is being investigated actively.

Potential.—The deposits in the Darling Range cover many square miles and have not yet been fully assessed. Reserves may amount to hundreds of millions of tons.

The new occurrence in the Kimberley should be of high grade and testing may show it to be a major deposit.

Iron.—Earlier geologists reported the occurrence of large deposits of iron in this State. Woodward in 1888, in a Government publication, stated that the north-west of this State would supply the world when other iron ore resources were exhausted. After 1950 an overseas market developed for iron ore and with the relaxation of the Commonwealth Government's export embargo at the end of 1960, exploration for iron ore became worthwhile. Immediately the north-west portion of this State became the focal point of extensive exploration by major companies and within 3 years the Hamersley Iron Province, as it is now known, was explored and assessed to be one of the major iron fields of the world.

The Hamersley Iron Province consists of a Proterozoic sedimentary succession containing thick and extensive banded iron formations, which are thought to have been deposited as chemical sediments from solutions rich in iron, silica, and carbonates. In general they are only gently folded and unmetamorphosed and contain between 20 and 40 per cent iron and between 40 and 60 per cent silica and carbonates. The most important formation for iron deposits is the Brockman Iron Formation, which is 2,000 feet thick and may originally have covered over 30,000 square miles.

The iron ore is thought to have been formed in structurally favourable localities by leaching of the silica and carbonates and the supergene enrichment of the iron over a long period of geological time. This process has produced large hematite-goethite ore bodies ranging in grade from 55 to 68 per cent iron.

A similar process, in the detritus deposited on the flanks of the banded iron formation and in the adjacent drainage channels, has resulted in the formation of limonite-goethite ores ranging from 50 to 60 per cent iron.

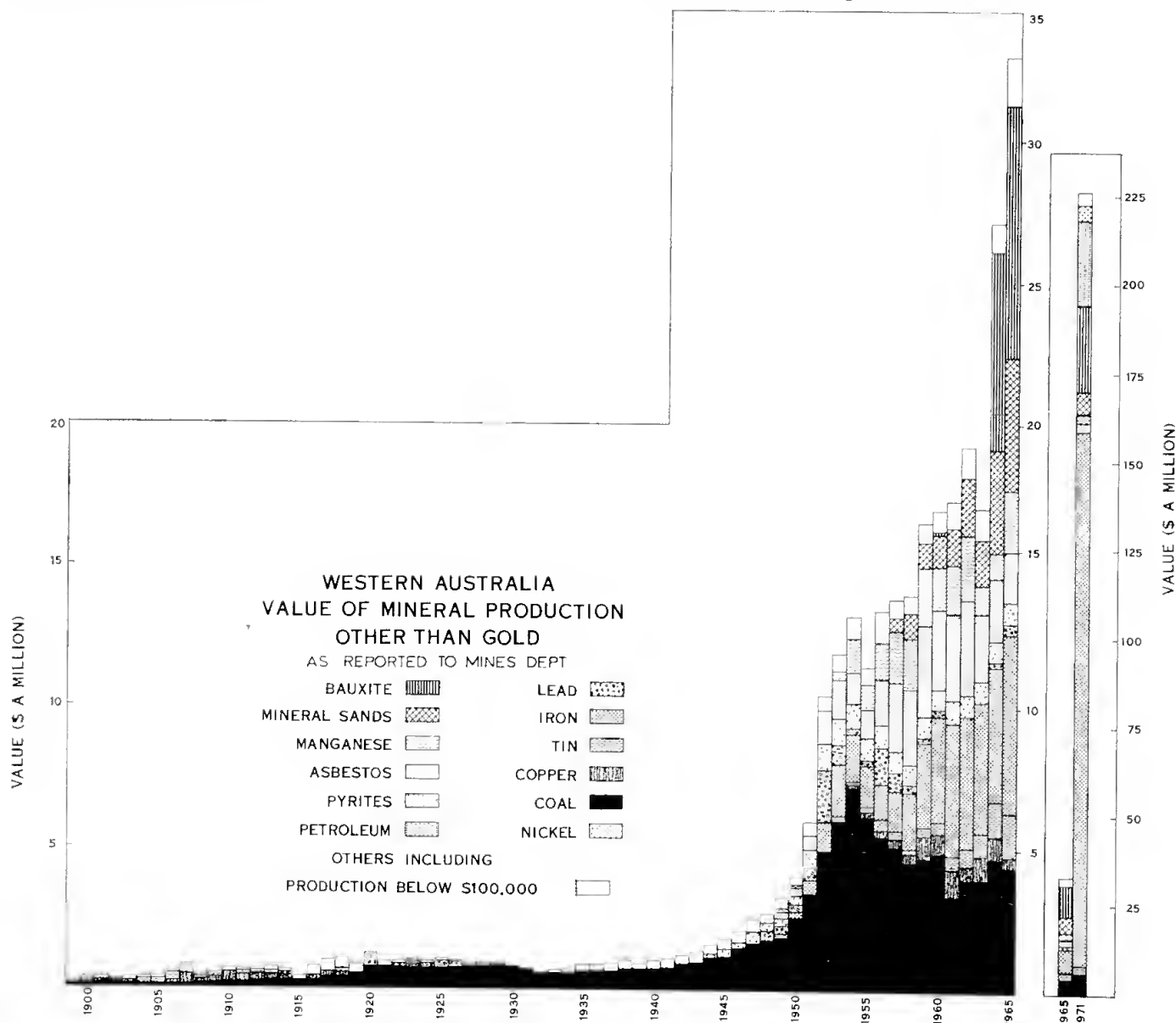


Fig. 4. Value of Mineral Production other than Gold, Western Australia, 1899-1965 with projection to 1971.

The Archaean rocks of this State contain steeply dipping and strongly folded iron formations, which have been subjected to deep and protracted erosion and metasomatic replacement. It appears that most of the iron ore deposits, which occur as massive concordant lenses, have originated by selective leaching of silica from jaspilite. These Archaean deposits are widely distributed over the north-western and southern portions of this region.

In the Kimberley Division occur iron ores of clastic sedimentary origin which were probably formed by the concentrating action of water along old shorelines. Such deposits occur at Yampi Sound, Pompeys Pillar and in the Bandicoot and Osmond Ranges.

Potential.—In the words of Woodward in 1888 there is "sufficient (iron ore) to supply the world". The inferred iron ore reserves of the State exceed 15,000 million tons, with an iron content of 50 per cent or more. About 8,000 million tons of this are high grade hematite ores with an iron content of 60 per cent or better. Over 1,000 million tons have been proven by drilling to average more than 64 per cent iron with low phosphorus content.

In the Hamersley Iron Province, where over 90 per cent of the ore reserves occur, at least 100 ore bodies have been recognized. The two major hematite deposits investigated and being developed are at Mt. Tom Price and Mt. Newman, each of which have reserves of over 500 million tons. Other hematite deposits occur at Mt. Brockman and Weeli Wolli Spring. The pisolitic-limonite-goethite ores are most abundant in the valleys of the Robe and Beasley Rivers and Duck Creek.

The Archaean hematite deposits are scattered widely over the State. Export of iron ore of this type has commenced from Koolanooka and Mt. Goldsworthy, and the Koolyanobbing deposit is being developed to supply ore to a blast furnace at Kwinana, near Perth. Deposits at Mt. Gibson, and Wilgie Mia in the Weld Range, are being investigated for export feasibility. These deposits range in size up to 70 million tons of high grade (60 per cent plus) ore and are in some places associated with larger tonnages of low grade ore. In the Kimberley region deposits at Yampi Sound have reserves estimated to be 78 million tons, while the other deposits located have not proved suitable for development as direct shipping ore. However, in the future they could be suitable for beneficiation and pelletization.

Asbestos.—Crocidolite (or blue asbestos), a fibrous variety of the alkali amphibolite riebeckite, occurs extensively in the Hamersley Range. It is mined at Wittenoom Gorge where seams range from $\frac{1}{4}$ to $2\frac{1}{2}$ inches in width and are interbedded with the cherty iron carbonate beds of the Brockman Iron Formation.

Chrysotile (or white asbestos) occurs at numerous localities in the Archaean rocks, particularly in the Pilbara and West Pilbara Goldfields. Production has been only on a minor scale.

Potential.—Providing satisfactory markets can be established and the present grade proved to be economical, there is a reasonable potential for the future development of blue asbestos

in the Hamersley Range, while exploration for white asbestos may locate deposits worthy of major development.

Manganese.—At present Western Australia has been Australia's major producer of manganese ore, but with the discovery of large continuous deposits on Groote Island this position may change shortly. Production in this State has been from the Pilbara area and from Horse-shoe near Peak Hill.

Usually the deposits are formed as a result of supergene enrichment of manganiferous sediments or by precipitation near the surface of manganese derived from the sediments. Rarely do they extend to depth, except in a few cases which, as they are the result of cavity filling, may have only a small surface expression and may continue to greater depths.

The ore bodies range in size from a few tons to several thousands, and in rare cases, hundreds of thousands of tons. Most of the ore bodies are in the 500 to 5,000 tons range with an average grade of 45 to 50 per cent manganese.

Potential.—Due to the nature of occurrence of manganese, mining has been spasmodic and remains in the hands of small operators. No alteration can be seen in the future.

Tin.—At Greenbushes, where tin was first discovered in 1888, cassiterite occurs in association with tantalite in veins in greenstone and granite, which has produced detrital accumulations in the overlying alluvium. A little lode tin has been mined.

In the Pilbara goldfield, cassiterite, derived from albitized pegmatites associated with Archaean rocks, occurs as eluvial or detrital accumulations near the host pegmatites or from alluvial concentrations in present and past drainage channels. Tantalite and columbite are common associate minerals.

Potential.—The tin deposits of this State are small and flourish only when the world market price is high, as at present. There does not appear to be any possibility of a major long term expansion in production.

Copper.—Copper deposits have been found throughout Precambrian rocks, mainly as narrow copper-gold-quartz veins in various types of metasediments and basic igneous rocks. Most deposits have been only small producers in the oxidized or secondary enriched zone. The grade in the primary zone has been too low to warrant development. The largest and richest mine, at Whim Creek, produced only 9,918 tons of metallic copper.

Potential.—With the large number of occurrences throughout the State, one must be optimistic that a major deposit will be located. The Bangemall Group in the Ashburton Valley may prove the host for such a find.

Lead.—Over 80 per cent of lead production in this State has come from the Northampton Mineral Field, where lead ore bodies occur in shear zones in gneiss associated with quartz veins. The lodes are not large or persistent, with the result that mining is on a small scale and most activity is restricted to periods of high world lead prices. Lead occurrences have been recorded from many localities throughout this region.

Potential.—Like copper, the prospects of finding a large lead deposit are considered reasonable and again the Bangemall Group in the Ashburton Valley is worthy of extensive and detailed prospecting.

Nickel.—The possibility of major nickel occurrences existing in this State has long been neglected, which is difficult to understand, considering the known wide occurrence of ultrabasic and serpentine rocks, which serve as hosts for nickel mineralization. In the late 1950s nickel mineralization was located near the eastern border of the State and at Wingellina, where it occurs as garnierite in laterite developed over ultrabasic rocks. Although the deposit is still being explored the geographical position makes development of a mine very difficult.

At Kambalda, 30 miles south of Kalgoorlie, an economic deposit of nickel sulphide in pyrrhotite was located recently in a structure near the contact of ultrabasic and serpentine rocks. This geological environment is being prospected actively by mining companies and some nickel mineralization has been located. Geophysical and geochemical anomalies indicate that further prospective zones exist.

Potential.—With one mine being developed, and favourable prospects of finding additional ore bodies, this State could become a major nickel producer.

Sedimentary basins

The Perth, Carnarvon, Canning, Bonaparte, Officer, and Eucla sedimentary basins together cover nearly 400,000 square miles of the State. Although extensively faulted in places, the sediments are not highly altered and only two small areas have igneous intrusions, one in the northern part of the Canning Basin and the other in the southern portion of the Perth Basin.

It is only in the last 15 years that the sedimentary basins have been investigated in a serious manner for possible mineral occurrences and, because of the large area involved in many instances, it has been necessarily in a very cursory manner.

Oil and Gas.—The first "oil boom" occurred in this State at the beginning of the century and the earliest oil wells were drilled near the Warren River at the south end of the Perth Basin. The next period of interest commenced in 1919 when traces of oil were found in a water bore on Gogo Station on the northern side of the Canning Basin. This resulted in the formation of the Freney-Kimberley Oil Company, which, operating spasmodically, drilled a number of unsuccessful holes in the Canning Basin, until taken over by another company in 1954. An American company commenced detailed investigations in the Canning Basin in 1940 and 1941 but ceased operations due to the War.

The first large-scale exploration, employing the full range of modern techniques, began in 1952 with the formation of West Australian Petroleum Pty. Ltd., commonly known as Wapet.

In their first hole, Rough Range No. 1, in 1953, oil was produced at a rate of 500 barrels per day from the lower Cretaceous sands of the Birdrong Formation at a depth of 3,602 feet. Subsequent drilling showed that this oil accumulation was too small for commercial development at that stage.

This initial success was followed by 11 years of fruitless search and it was not until 1964 that the company made another significant discovery when oil and gas were found on Barrow Island and also near Yardarino. More recently, oil and gas have been found at Mt. Horner and at Gingin, Arrowsmith and Dongara, all in the northern portion of the Perth Basin.

The Barrow Island discovery has been declared commercial and production is planned from the top oil horizon, the Lower Cretaceous Windalia Radiolarite at the depth of 2,500 feet. This formation lacks permeability and modern fracturing techniques will be used to recover the oil. Upon the success of this technique depends the final quantity of oil which will be recovered. The very conservative estimate of the recoverable reserve is 85 million barrels which will give a productive life to this horizon of about 12 years at the present rate of production.

Deeper Jurassic formations between 6,000 and 7,500 feet are structurally more complicated and the full assessment of their oil potential has yet to be completed. It is known that the sands are more productive and contain a variable amount of gas, but the area of sands present is probably much less than the higher horizon.

Potential.—With Barrow Island commencing production in 1967 and favourable indications found in some other areas, one must be optimistic that more fields will be discovered. Only 177 drilled holes of all types, of which 26 are on Barrow Island, have been put down for oil search in this State. When the area of sedimentary rocks is considered it is easy to realize that the search is only just beginning.

Although a gas field has not yet been defined, the prospects in the northern part of the Perth Basin are very good. The time may not be far distant when a gas pipe line network covering the State from Geraldton to Bunbury may be a possibility, providing cheap power and supplying a petro-chemical industry producing fertilizers, plastics, sulphur and other products at some convenient point.

Coal.—Despite the large area of sedimentary basins, this State does not possess good coal resources. The only source of commercial coal is at Collie, a small Permian basin within the Precambrian shield area.

The Collie coal basin covers about 90 square miles and contains three horizons of coal seams. The strata are poorly consolidated sandstones and shales, which have been affected severely by slumping and faulting. As a result, underground mining costs are high and operations difficult and collieries are usually abandoned for these reasons, rather than the lack of coal.

The coal is of low rank, black, non-coking, sub-bituminous and with a calorific value of about 9,000 B.Th.U. as mined today. One feature is the low ash content of 2 to 4 per cent.

Collie coal has been the State's principal source of power since production began in 1898 but because of rising costs it is now used only for the generation of electrical power, which consumes nearly 1 million tons per year. The only coal of better quality located in this State was in the Eneabba No. 1 oil well in the northern portion of the Perth Basin at a depth of

over 6,000 feet. It was a lower Jurassic coal with a calorific value of about 12,000 B.Th.U. Exploration failed to locate this coal at shallower depths.

Potential.—There are indicated extractable reserves at Collie, at the present rate of consumption, for the next 50 to 100 years. However, rising costs will have to be halted or otherwise natural oil or gas may capture the power market.

There are still possibilities that sub-surface deposits of coal may be found in other basins.

Mineral Sands.—Mineral sands deposits in the southern portion of the Perth Basin near Bunbury and Busselton have been located and developed in recent years. The establishment of this industry has not been rapid due to the low market price of the principal mineral, ilmenite. Zircon and small amounts of rutile and monazite occur also in the heavy mineral concentrate.

These minerals occur as minor accessory minerals in the Precambrian granitic rocks of the south-west portion of the State. Protracted erosion has liberated large quantities of these accessory minerals, which have found their way to the sea, where its action has concentrated them along strand lines. Due to a number of small uplifts of the coast, the old strand lines with associated heavy mineral concentrations, are now found some distance inland.

Potential.—The reserves held by the operating companies appear adequate for some years allowing for a gradual increase in the production rate.

Continental shelf

There is a mounting interest throughout the world in the search for minerals offshore on the continental shelf and slope. This State with its long coastline and wide shelf, particularly in the north, has a potential search area in excess of 200,000 square miles.

Offshore exploration so far has been confined to airborne magnetometer and marine seismic surveys for petroleum. Within the next 2 years offshore drilling for oil and sampling of the sea floor for minerals should begin. These investigations will be costly but must be attempted and encouraged if this State is to keep abreast of modern trends in exploration.

Potential.—The petroleum potential offshore is encouraging and it is almost certain, as a result of Barrow Island discoveries that further

oil fields will be located offshore, particularly from Exmouth Gulf northwards and in the Joseph Bonaparte Gulf.

Other minerals which may be found offshore include phosphates, manganese, tin and ilmenite.

Salt will soon be produced on a major scale at Shark Bay, Port Hedland and Dampier by pumping sea water into constructed evaporating pans on the coastal flats.

The future

The potential of minerals now in production and others which may be produced within the next few years have been discussed. No doubt there are minerals in this State which are of no economic importance at present but which may assume importance in the future; there are also minerals whose occurrences have been recorded but to which as yet insufficient attention has been paid by exploration companies. These include chromium, vanadium, molybdenum and uranium. Amongst the non-metallic minerals, it is hoped that phosphate will be located in economic quantities, and the evaporite formations, located during oil drilling, may disclose commercial deposits of potassium and other salts when examined in detail.

The mineral production of this State is about to undergo a dramatic increase from a total value of \$A53.8 million last year (1965) to a possible \$A245 million in 1971, as shown in Figs. 2, 3 and 4. This estimate takes into account only the planned and proposed developments. There is no doubt that the major developments in iron, bauxite, petroleum, nickel and mineral sands will stimulate the exploration and development of other mineral deposits.

The Table below shows how the value of production of various minerals may develop and how by the end of 1971 minerals could become the leading money earning industry in this State. In future iron will displace gold as our major mineral and statistics may have to be shown as "iron" and "minerals other than iron".

Acknowledgements

The information used in this address has been drawn from numerous reports of the Geological Survey of Western Australia, by many authors. The statistics were supplied by the Statistical Branch of the Mines Department.

Mineral production of Western Australia
(\$1Aust. = \$1U.S. = £0.625 Sterling)

Mineral	1953 \$A actual	1965 \$A actual	1971 \$A estimate
Gold	26,598,000	20,722,000	18,500,000
Bauxite	—	8,908,000	24,000,000
Iron	1,806,000	6,316,000	150,000,000
Mineral Sands	—	4,744,000	6,500,000
Coal	6,146,000	4,410,000	5,500,000
Manganese	302,000	2,152,000	2,500,000
Asbestos	1,414,723	1,804,000	2,500,000
Tin	126,000	1,557,000	2,500,000
Pyrite	980,000	768,000	750,000
Lead	148,000	393,000	400,000
Copper	48,000	334,000	500,000
Petroleum	—	—	24,000,000
Nickel	—	—	4,000,000
Others (inc. salt)	1,089,000	1,697,000	3,850,000
Total	38,657,000	53,825,000	245,000,000

5.—The order of cusp development on the molar teeth of *Setonix brachyurus* (Macropodidae: Marsupialia)

by B. K. B. Berkovitz*

Manuscript received 15 March 1966; accepted 19 July 1966

Abstract

The order of cusp development and cusp calcification in the upper deciduous premolar of *Setonix*, and most probably the upper first molar, resemble that occurring in placentals, the paracone representing the primary cusp. The primary cusp in the lower deciduous premolar of *Setonix*, and perhaps also in the lower second molar, was the metaconid, differing from that of placentals, while in the lower first molar the primary cusp was the protoconid. During the early stages of tooth development the upper deciduous premolar and first molar were more advanced in their development than the corresponding lower teeth.

Introduction

A detailed study of the order of cusp development on the cheek teeth of the Macropodidae has never been carried out and little information is to be found concerning cusp development in other marsupials. In some marsupials, namely *Myrmecobius*, *Peragale* (*Macrotis*) and *Phascogale*, Woodward (1896) found the upper primary cusp to be the paracone and the lower primary cusp to be the protoconid. According to Röse (1892), the metacone of the upper deciduous premolar of *Didelphis* calcified before the paracone, while the first cusp to be added to the protoconid of the lower teeth was the metaconid. In the first upper molariform tooth of a specimen of *Perameles*, Bolk (1917) found the paracone, protocone and metacone present, the former two cusps being calcified.

The lower deciduous premolar of certain members of the Phalangerioidea, e.g. *Hypsiprymnodon*, possesses real evidence of only one anterior cusp which is generally displaced lingually, giving the tooth a wedge-shaped appearance when viewed from above; the homology of this anterior cusp is the subject of dispute (Ride 1961). The determination of the homology of the cusps of the lower deciduous premolar in *Setonix brachyurus*, which is similarly wedge-shaped, possessing a prominent antero-lingual cusp and a greatly reduced antero-buccal cusp, may help to indicate the homology of the single anterior cusp in other members of the Phalangerioidea.

The dentition of *Setonix brachyurus*

The animal used for the present study was *Setonix brachyurus*, the quokka of Western Australia.

Simpson (1945) placed *Setonix* in the Superfamily Phalangerioidea, Family Macropodidae, and the Subfamily Macropodinae. Other classifications have been suggested by Thomas (1888),

Bensley (1903), Gregory (1910), Jones (1924), Raven and Gregory (1946), Tate (1948) and Ride (1957, 1964). *Setonix* may be regarded as representing a monotypic genus related to the wallabies. Recent work by Sharman (1954) on the chromosome structure and the urino-genital characteristics of *Setonix* have led him (1961) and Ride (1957) to consider the possibility that *Setonix* may be more closely related to the rat-kangaroos than to the more advanced Macropodinae.

The dental formula of *Setonix*, excluding the deciduous premolar, is:— $I^{3/1} C^{0/0} Pm^{2/2} M^{1/1}$, and is characteristic of members of the Macropodinae. Owing to its large size, the replacing premolar in *Setonix* replaces the anterior premolar in addition to the deciduous premolar, so that only one sectorial premolar is functional at a time.

Setonix resembles the wallabies and differs from the true kangaroos in possessing:

- (a) large sectorial premolars which remain functional throughout life,
- (b) a fourth molar tooth which is slightly smaller than the third,
- (c) a comparatively small upper third incisor.

Setonix also possesses large posterior palatal vacuities, and a large masseteric canal the size of which appears to be related to the size of the sectorial premolars (Ride 1959).

The terminology used for the transverse ridges of the teeth is that given by Scott and Symons (1958).

Morphology of the molar teeth

Upper jaw (Fig. 1, left)

The anterior and posterior pairs of cusps have united to form two transverse ridges or lophs. The anterior loph or paraloph is formed by the union of the anterior pair of cusps, the buccal paracone and lingual protocone, while the posterior loph or metaloph is formed by the union of the posterior pair of cusps, the buccal metacone and lingual hypocone. The two lophs are united by a narrow longitudinal ridge. The lophs are curved with the convexity facing anteriorly. A small anterior cingulum is present.

The molar teeth show a general increase in size from before backwards, but the third molar is slightly larger than the fourth. The fourth molar lies more lingual than the third, so that the toothrow curves towards the sagittal plane at its posterior end.

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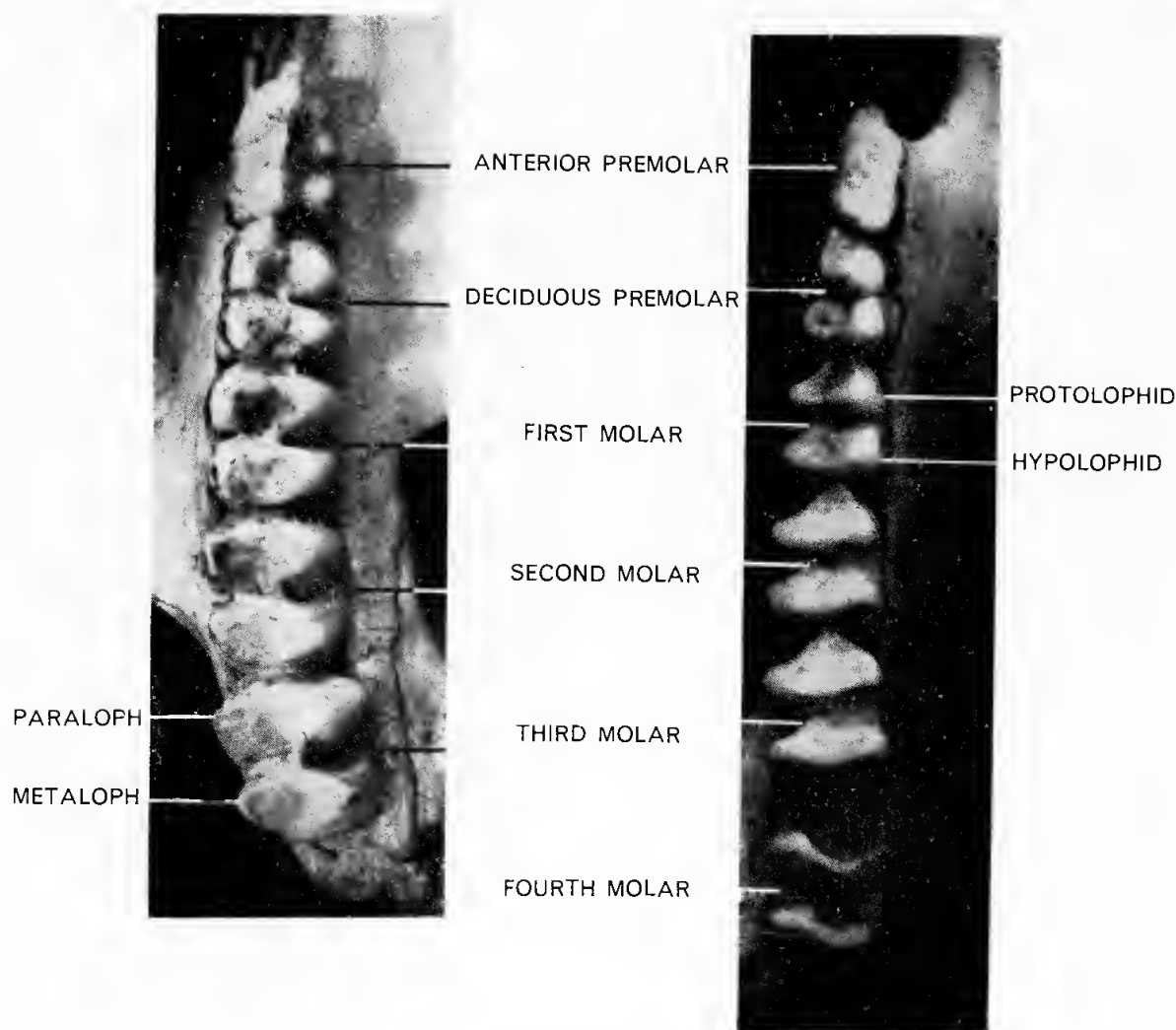


Figure 1.—(Left hand side) Upper right anterior cheek teeth, x3.8. (Right hand side) Lower left cheek teeth, x3.5.

In the case of the deciduous premolar the paraloph is not as well developed as in the other molar teeth, a shallow groove being present on the anterior as well as the posterior surface, and the anterior margin of the paracone rises to form a conspicuous ridge which is functionally continuous with the median longitudinal ridge of the anterior premolar.

Lower jaw

The anterior and posterior pairs of cusps combine to form two transverse ridges or lophids. The anterior lophid or proto-lophid is formed by the anterior cusps, the buccal protoconid and lingual metaconid, while the posterior lophid or hypolophid is formed by the posterior cusps, the buccal hypoconid and lingual entoconid. The two lophids are united by a narrow longitudinal ridge. The lophids are curved with the convexity facing posteriorly, this being opposite to the condition found in the upper molars. The anterior margin of the protoconid rises to form a narrow ridge. The relative size and position of the lower molar teeth are similar to the upper molars.

In the case of the deciduous premolar the proto-lophid is greatly diminished in its buccolingual dimension due to the reduction in size of the protoconid, giving the tooth a wedge-shaped outline when viewed from above.

Materials and methods

Table 1 lists the pouch young specimens of *Setonix* used in the study together with their accompanying data.

TABLE 1

List of pouch young specimens of *Setonix brachyurus* used in the present study.

Specimen and Stage No.	Estimated Age from Birth (days)	Body-weight (grams)	Snout-occiput Length (mm)
1	< 7	0.69	8.5
2	< 11	1.153	10.1
3	25	3.0	12.1
4	30	4.5	16.1
5	40	8.0	19.1
6	46	10.0	21.8
7	52	16.0	25.5

As the specimens were obtained during reproductive studies by other workers, their ages were known. The specimens had been fixed in Baker's formol-calcium and preserved in 70% alcohol. X-rays revealed that no decalcification was necessary prior to sectioning. Sectioning was carried out in a transverse plane using a rotary microtome set to cut at 10μ , the heads being embedded in wax. Masson's trichrome was the stain used. Predentine could be distinguished from mature dentine according to the colour of the staining reaction.

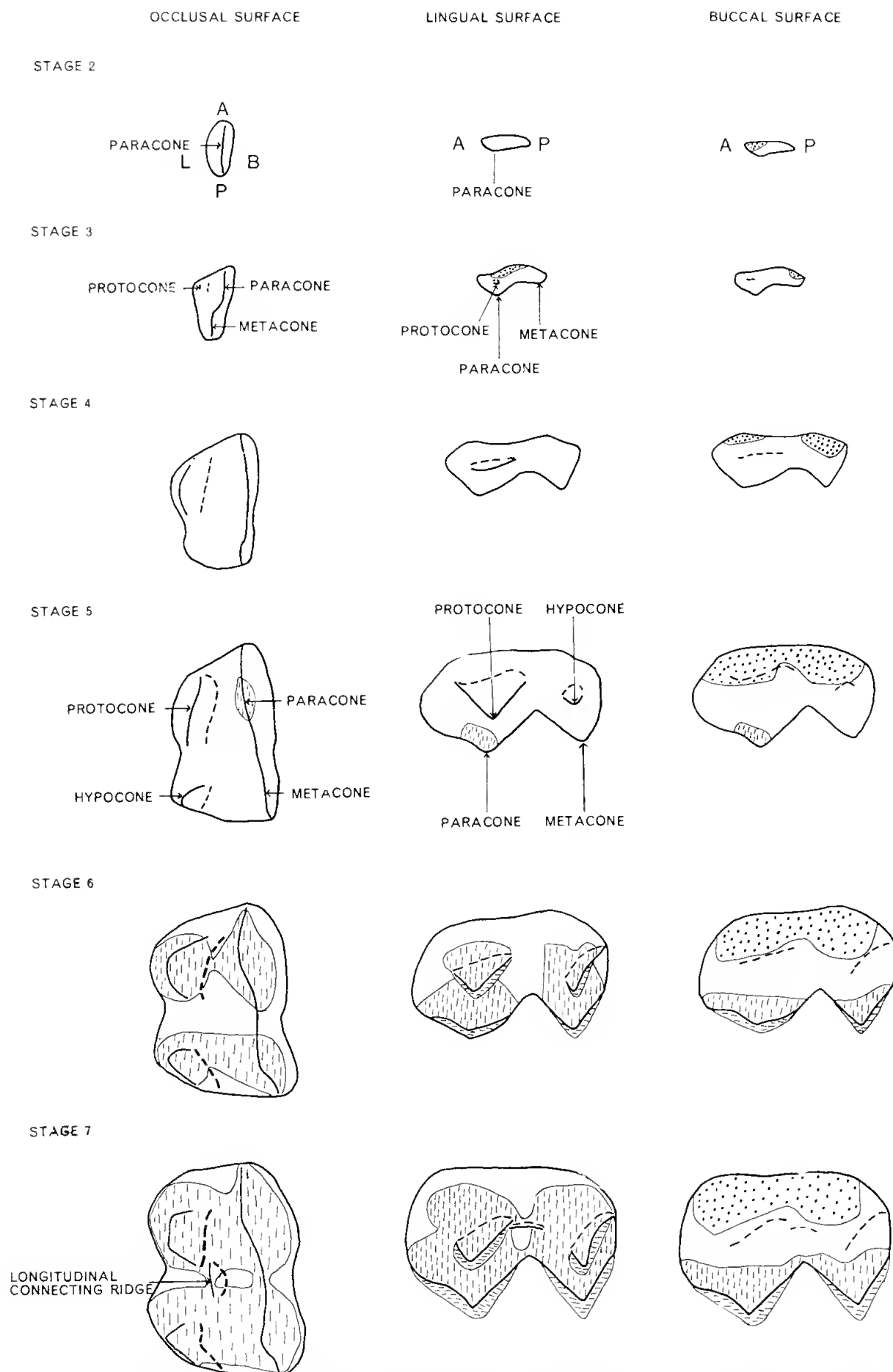


Figure 2.—Development of the upper deciduous premolar. Stages 2-5 x12.5, stages 6 and 7 x10. In all figures: A = anterior, B = buccal, L = lingual, P = posterior, vertical line stipple = dentine, horizontal line stipple = enamel, heavy dot stipple = pulp aperture.

Reconstructions of the teeth were carried out by the graphical method in occlusal and side views, and where necessary supplemented by the construction of three-dimensional wax models. The techniques and precautions taken for these reconstructions were identical to those adopted by Aldridge (1962), using the base of the wax block as a guide line.

Results

Cusp development in the molar teeth

The deciduous premolar was first seen developing from the free edge of the dental lamina at the posterior end of the developing jaw at stage 1. The first molar developed behind the deciduous premolar and was continuous anteriorly with the residual dental lamina lying

to the lingual side of the deciduous premolar. The second molar developed behind the first molar and was continuous anteriorly with the residual dental lamina lying to the lingual side of the first molar.

Upper Jaw

Deciduous Premolar (Fig. 2). This tooth reached the cap stage of development at stage 2. The first cusp to develop was the paracone which was clearly visible at stage 3. Although traces of the protocone and metacone were observed at stage 3, these cusps first became conspicuous at stage 4, having developed at approximately the same time. The last cusp to develop was the hypocone which appeared at stage 5.

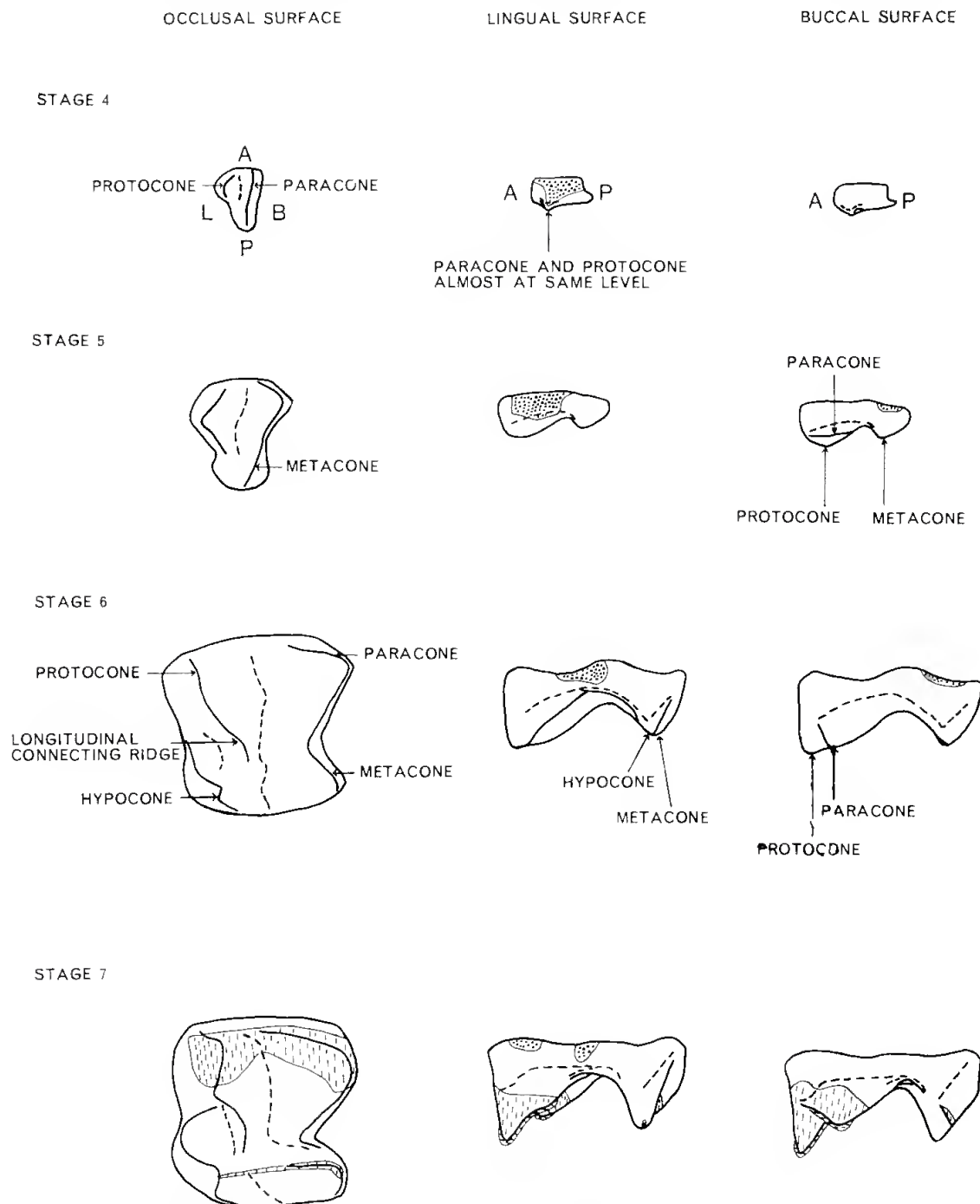


Figure 3.—Development of the upper first molar. Stages 4-6 x12.5, stage 7 x10. For key see caption of Figure 2.

The first cusp to calcify was the paracone, which at stage 5 possessed a layer of dentine at its apex. At stage 5 a small amount of predentine had been deposited at the apex of both the protocone and metacone, indicating that these two cusps commenced the process of calcification after the paracone and at approximately the same time as each other. The last cusp to calcify was the hypocone at stage 6.

First Molar (Fig. 3). The cap stage of development for this tooth was reached at stage 3. At stage 4 two cusps were present on the crown, corresponding to the paracone and protocone; the paracone was slightly more prominent and, developing from the main ridge, almost certainly represented the primary cusp. The third cusp to develop was the metacone which appeared at stage 5. The last cusp to develop, the hypocone, was seen initially at stage 6.

At stage 6 predentine had been formed in the apical region of both the protocone and paracone, the presence of a very small amount of dentine on the paracone indicating that the paracone probably commenced calcification just before the protocone. At stage 7 a small amount of dentine had been formed at the apex of both the metacone and hypocone and along the crest of the metaloph, most of this dentine being associated with the apex of the metacone, indicating that the metacone was the third cusp, and the hypocone the last cusp to calcify.

Second molar. This tooth reached the cap stage of development at stage 6. At stage 7 the enamel organ of the tooth was still small, although traces of three low cusps apparently corresponding to the paracone, protocone and metacone, were present on the crown.

Lower jaw

Deciduous Premolar (Figs. 4 & 5). The cap stage of development of this tooth was reached at stage 2. At stage 4 three cusps, namely the metaconid, protoconid and hypoconid, were present on the crown, and of these cusps the

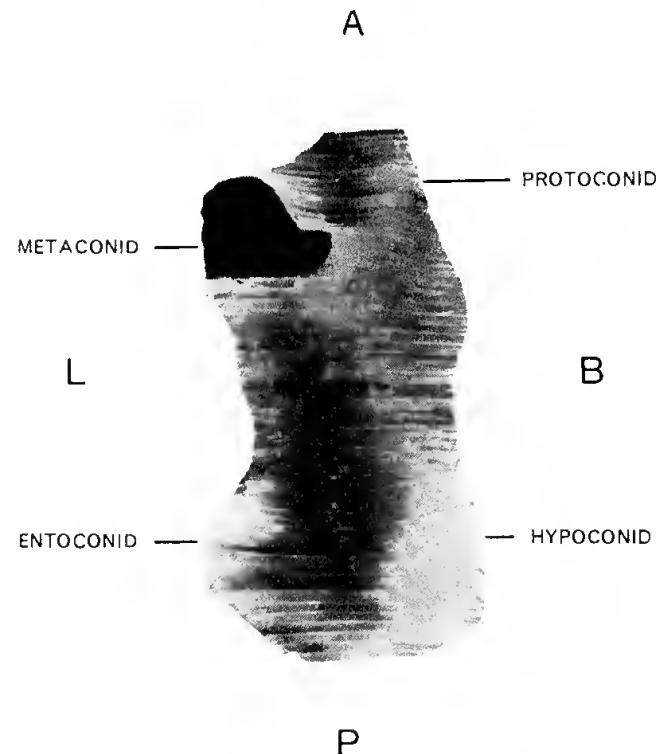


Figure 4.—Wax reconstruction of the lower deciduous premolar at stage 5, x34. Black area indicates dentine formation.

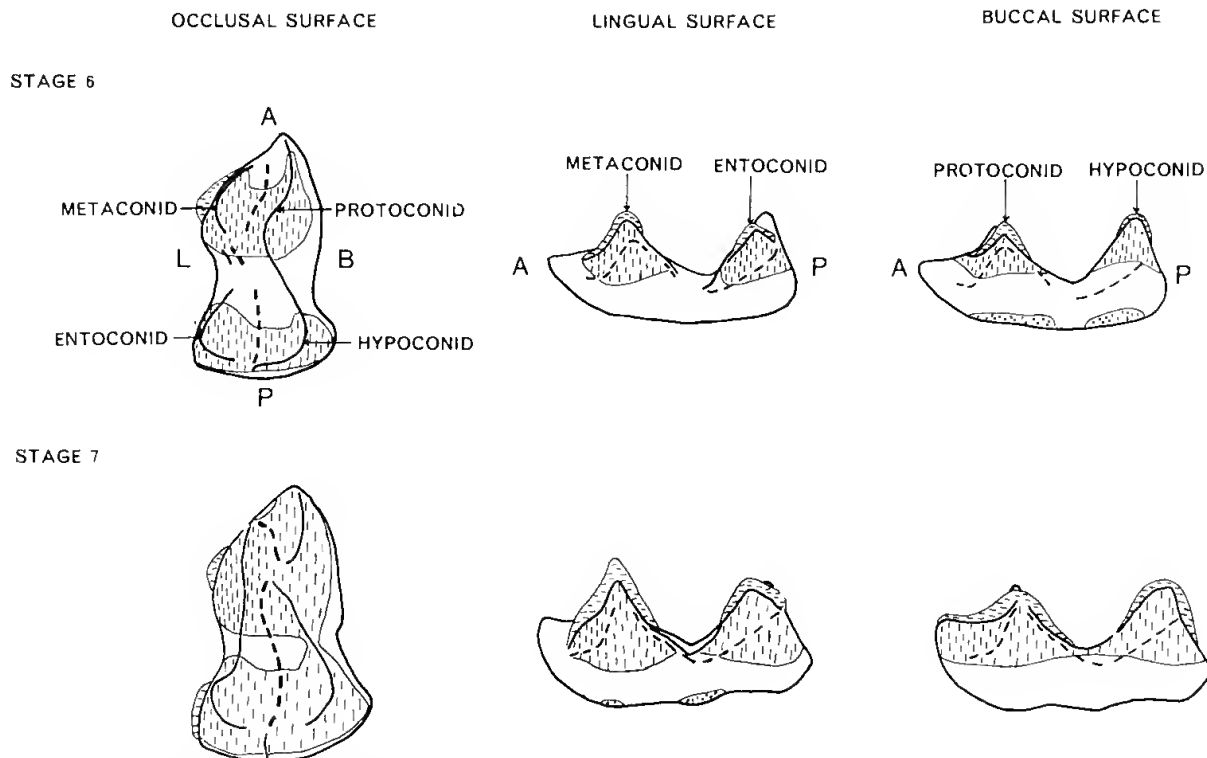


Figure 5.—Development of the lower deciduous premolar at stages 6 and 7, x10. In lateral views only the calcified tissue associated with the nearest cusp is illustrated. For key see Figure 2 caption.

metaconid was by far the most prominent. The last cusp to develop was the entoconid which appeared at stage 5.

The first cusp to calcify was the metaconid which possessed a conspicuous layer of dentine at stage 5. At stage 5 the protoconid contained a layer of predentine which was continuous along the crest of the protolophid with the predentine layer associated with the metaconid. This indicated that the protoconid was the second cusp to commence calcification. The hypoconid and entoconid were the last cusps to calcify, both being calcified at stage 6.

First Molar (Fig. 6). This tooth reached the cap stage of development at stage 3. At stage 5 three cusps were present on the crown, namely the protoconid, metaconid and hypoconid. The protoconid, lying anterior to the metaconid, was slightly more prominent than the other cusps. The last cusp to develop, the entoconid, appeared at stage 6.

At stage 6 predentine had been deposited in the apical region of both the protoconid and metaconid, the greater quantity of predentine being associated with the protoconid, indicating that the protoconid commenced the process of calcification slightly before the metaconid. At stage 7 the apical region of the hypoconid contained a thin layer of dentine which extended across the crest of the hypolophid to become continuous with dentine at the apex of the entoconid. The greater amount of dentine associated with the hypoconid indicated that the hypoconid was the third cusp, and the entoconid the last cusp to calcify.

Second molar. This tooth reached the cap stage of development at stage 6. At stage 7 only two cusps were present on the crown, apparently corresponding to the metaconid and protoconid, the metaconid being the more prominent cusp.

The order of cusp development and cusp calcification on the molariform teeth in *Setonix* is summarised in Tables 2 and 3.

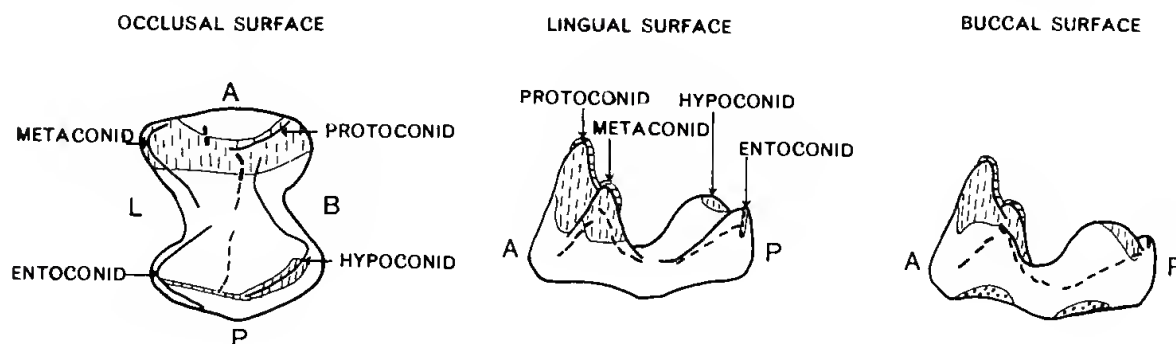


Figure 6.—Lower first molar at stage 7, x10.

Discussion

Development of upper molars

The main difference between the development of the deciduous premolar and the first molar is the accelerated development of the protocone which occurs in the first molar and which is probably associated with the more completely formed paraloph present in the first molar.

The order of cusp calcification appears to be closely related to the order of cusp development which resembles that occurring in placentals, the paracone representing the primary cusp and the hypocone being the last cusp to develop (Butler 1956).

Development of lower molars

A most important difference is observed between the development of the deciduous premolar and the first molar, for while the protoconid is slightly more prominent than the metaconid and is the first cusp to calcify on the first molar, the situation is reversed in the deciduous premolar where the metaconid is much more prominent than the protoconid and is the first cusp to calcify. This difference in development appears to be related to the small size of the protoconid on the deciduous premolar.

TABLE 2

Order of cusp development and cusp calcification in the upper jaw of Setonix brachyurus.

	DECIDUOUS PREMOLAR	FIRST MOLAR	SECOND MOLAR
ORDER OF CUSP DEVELOPMENT	1. Paracone (stage 3) 2. Protocone, Metacone (stage 4) 4. Hypocone (stage 5)	1. Paracone, Protocone (stage 4) 3. Metacone (stage 5) 4. Hypocone (stage 6)	1. Paracone, Protocone, Metacone? (stage 7)
ORDER OF CUSP CALCIFICATION	1. Paracone (stage 5) 2. Protocone, Metacone (stage 5) 4. Hypocone (stage 6)	1. Paracone, Protocone (stage 6) 3. Metacone (stage 7) 4. Hypocone (stage 7)	

TABLE 3

Order of cusp development and cusp calcification in the lower jaw of Setonix brachyurus.

	DECIDUOUS PREMOLAR	FIRST MOLAR	SECOND MOLAR
ORDER OF CUSP DEVELOPMENT	1. Metaconid (stage 4) 2. Protoconid, Hypoconid (stage 4) 4. Entoconid (stage 5)	1. Protoconid, Metaconid Hypoconid (stage 5) 4. Entoconid (stage 6)	1. Protoconid, Metaconid? (stage 7)
ORDER OF CUSP CALCIFICATION	1. Metaconid (stage 5) 2. Protoconid (stage 5) 3. Hypoconid, Entoconid (stage 6)	1. Protoconid (stage 6) 2. Metaconid (stage 6) 3. Hypoconid (stage 7) 4. Entoconid (stage 7)	

If the early height of a cusp and the time of its calcification relative to that of the other cusps are expressions of the order in which cusps develop in the first place, then the primary cusp in the deciduous premolar is the metaconid while that in the first molar is the protoconid. Thus, in *Setonix*, not only is there a difference in the order in which cusps calcify on the crowns of these two teeth, but this might be held to indicate that the primary cusps in them are different, the primary cusp in the deciduous premolar being the metaconid and in the first molar the protoconid. Such a conclusion would also mean that the primary cusp in the deciduous lower premolar of *Setonix* differs from that of the typical lower molar of placentals where the primary cusp is the protoconid (Butler 1956).

As an alternative explanation, however, the late calcification of the protoconid of the deciduous tooth, or the precocious calcification of the metaconid, might be only an expression of the much reduced size of the protoconid in the deciduous premolar of *Setonix*. Thus, in the deciduous premolar, the protoconid could develop first but the metaconid appearing later would soon outstrip the protoconid in development, rapidly becoming the most prominent cusp and reaching the stage of calcification earlier. If this is true, then the early height of a cusp and its time of calcification, which normally allow the identification of the primary cusp, need not necessarily indicate the correct order of cusp development (see Butler 1956). The order of cusp development can only be determined if a series of specimens is obtained clearly showing the cusps developing one after another; the difficulty in obtaining such a series is considerable, especially in cases where two or more cusps appear almost simultaneously.

In the oldest specimen examined in the present study, i.e., stage 7, the crown pattern of the lower second molar was incomplete and only two cusps were present on the crown. The homology of these two cusps cannot be determined with certainty unless further study is carried out on older specimens. However, it is suggested that these two cusps represent the protoconid and metaconid, the metaconid being the most prominent. If the early height of a cusp is a factor which may indicate the order of cusp development, then the metaconid may represent the primary cusp. This interpretation

would involve accepting a difference in the order of cusp development between the first and second molars, the primary cusp in the first molar being the protoconid and in the second molar, the metaconid. The alternative interpretation is that the protoconid is the first cusp to develop, but the metaconid, which appears after the protoconid, develops at a greater rate than the primary cusp and becomes more prominent. This latter interpretation would account for the apparent difference in development between the first and second molars but, as in the case of the deciduous premolar, would indicate that the early height of a cusp is a factor which does not denote the order of cusp development. Although the order of cusp development in the second molar may resemble that of the deciduous premolar, this cannot be confirmed until older specimens are examined.

The features of the lophs and lophids of the upper and lower molar teeth of *Setonix* were conspicuous as soon as the constituent cusps were present on the crown.

The accelerated development and calcification of the metaconid in the lower deciduous premolar may be regarded as positive factors favouring Ride's (1961) cuspal nomenclature of the lower cheek teeth of *Hypsiprymnodon* in which the main anterior cusp in the lower deciduous premolar is regarded as being the metaconid. The initial results of a study of the development of the cheek teeth of *Trichosurus vulpecula* carried out by the author support Ride's views.

A comparison between the development of the corresponding upper and lower molar teeth

Deciduous premolars. During the early stages the upper deciduous premolar is seen to be at a more advanced stage of development than the lower deciduous premolar. At stage 3 the paracone is conspicuous on the crown of the enamel organ of the upper deciduous premolar and the protocone and metacone are about to appear, while upon the smaller enamel organ of the lower deciduous premolar no cusps are visible. At stage 4 the enamel organs of both teeth possess three cusps, the paracone, metacone and protocone being present in the upper tooth, and the metaconid, protoconid and hypoconid being present in the lower tooth. At stage 5 four cusps are present in both teeth. Calcification

has commenced in the upper tooth with the formation of dentine at the apex of the paracone and predentine at the apex of the protocone. In the lower tooth calcification has also commenced, but dentine is formed on the metaconid, while only predentine is present on the protoconid. Predentine has also been formed on the metacone of the upper tooth at stage 5, but has not been formed on either of the posterior cusps of the lower tooth. At stage 6 both upper and lower teeth are at approximately the same stage of calcification, enamel and dentine being present on all four cusps.

First molars. At stage 4 the enamel organ of the upper tooth exhibits two low cusps on the crown, the paracone and protocone, while the ridge of the enamel organ of the lower tooth shows no cuspal elevations. In later stages the two teeth are at approximately the same stage of development.

Second molars. As in the oldest specimen examined, i.e., stage 7, these teeth were still only present as small enamel organs with incomplete crown patterns, no comparison will be made between them.

During the early stages the upper deciduous premolar and first molar are more advanced in their development than the corresponding lower teeth. In this respect *Setonix* differs from the Microchiroptera where Aldridge (1962) found that it was the lower molar teeth which were in a more advanced stage of development than the corresponding upper molar teeth.

Summary

- (1) The order of cusp development on the molar teeth was studied in a transversely sectioned series of pouch young of *Setonix brachyurus*.
- (2) The order of cusp development and cusp calcification in the upper deciduous premolar, and most probably the upper first molar, resembled that occurring in placentals, the paracone representing the primary cusp.
- (3) The primary cusp in the lower deciduous premolar, and perhaps also in the lower second molar, was the metaconid, while in the lower first molar the primary cusp was the protoconid.
- (4) During the early stages of tooth development the upper deciduous premolar and first molar were more advanced in their development than the corresponding lower teeth.

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I am also indebted to the Authorities of the British Museum (Natural History) for access to preserved specimens.

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6.—Geographic races of the agamid lizard *Amphibolurus caudicinctus*

by G. M. Storr*

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Abstract

Amphibolurus caudicinctus (Günther) occupies rocky habitats in the western two-thirds of Australia, north of latitude 29°S. It breaks up into at least 7 subspecies: *caudicinctus* (syn. *imbricatus* Peters), *mensarum* nov., *infans* nov., *graafi* nov., *rufescens* Stirling & Zietz, *slateri* nov., and *macropus* nov. Other populations, not yet identified to subspecies, are mentioned. Some aspects of the species' ecology are discussed, including evidence that members of the nominate race live for little more than a year.

Introduction

Amphibolurus caudicinctus is abundant in the rocky hills of the Pilbara-Hamersley region of Western Australia (which includes the type-locality). Elsewhere it is not so continuously distributed and is much less plentiful, at least in collections. It has therefore not been easy to characterise the numerous, more or less disjunct populations beyond the range of the nominate race, or to fix their geographic limits. This attempt to do so will doubtless require amendment as material from critical areas becomes available.

The races described herein are based almost entirely on adult male characters. In females and juveniles, geographic variation in colour pattern is largely obscured by individual variation and ontogenetic change. As a result, samples lacking fully adult males have generally not been determinable to subspecies.

In the following descriptions snout-vent length has been abbreviated to SVL. Numbers in brackets after ranges in quantitative characters are means. Measurements (summarised in Table 1) were made as in Storr (1965, p. 52). Upper labials were counted along the series of rectangular scales to the point where the outline of the lip begins to deflect downwards and backwards to the rictus; the irregularly shaped and sized scales posterior to this point were excluded.

The prefixes R, NTM, SAM and USNM refer to specimens respectively in the collections of the Western Australian Museum; Animal Industry Branch, Northern Territory Administration, Alice Springs; South Australian Museum, Adelaide; and Smithsonian Institution, Washington. For the loan of these external specimens I am indebted respectively to Mr. K. R. Slater, Mr. F. J. Mitchell and Dr. J. A. Peters. I am grateful to Mrs. A. Neumann (Librarian, Western Australian Museum) for translations of Peters' and Sternfeld's papers.

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General description of *A. caudicinctus*

Limbs and tail long (see Table 1). Nuchal crest a series of small, contiguous, laterally compressed spines. No dorsal crest (though a slight mid-dorsal ridge may be formed by perfectly aligned keels of enlarged, slightly raised, vertebral scales). Nostril much nearer to orbit than tip of snout, located on or immediately below swollen rostral ridge (acute in *rufescens*), entering downwards and slightly forwards. Strong gular fold extending obliquely back on to side of neck. No dorsolateral fold (except possibly in *rufescens*).

Scales on top of head unicarinate, becoming small and subtubercular on occiput. Dorsal scales small to moderately large, increasing in size towards enlarged vertebral series, imbricate, mucronate or spinose, strongly or weakly unicarinate, alignment of keels converging back towards midline. Lateral scales much smaller, arranged in transverse whorls, weakly imbricate, smooth or weakly unicarinate, their keels (when present) directed backwards and downwards. Scales on upper surface of limbs similar to but larger than dorsals. Gular and ventral scales weakly imbricate, smooth or feebly keeled.

Upper labials 12-19. Subdigital lamellae bispinose, 21-35 under fourth toe. Femoral and preanal pores in both sexes and all ages, 23-62, each located between a slightly raised clump of 4-5 scales, extending nearly to end of thigh and interrupted at midline.

Key to adult males

1. Nasal well below acute rostral ridge; pores more than 44 *rufescens*
Nasal on or just below swollen rostral ridge; pores fewer than 43 2
2. Whole of tail compressed; dark narrow caudal bands encircling tail *caudicinctus*
Base of tail not compressed; dark caudal bands (if any) not extending to lower surface 3
3. Adpressed hind-leg not extending to end of snout 4
Adpressed hind-leg extending past snout *macropus*
4. Keels of dorsal scales sharp and black *slateri*
Keels of dorsal scales obtuse and not black 5
5. Back reddish; hind-leg and base of tail obscurely banded with dark brown 6
Back yellowish; hind-leg and base of tail not banded *graafi*
6. Paravertebral spots obsolescent *mensarum*
Paravertebral spots persistent *infans*

TABLE 1

Mean length of head, tail, foreleg and hindleg, expressed as per cent. length of trunk; and mean width of head, depth of head and diameter of ear-aperture, expressed as per cent. length of head (all with standard deviations in brackets).

	Sample Size	Per cent. Length of Trunk				Per cent. Length of Head		
		Head	Tail	Foreleg	Hindleg	Head Width†	Head Depth	Ear
<i>caudicinctus</i>	37 ♂	41.5 (2.2)	321 (17)	62.2 (3.7)	127.2 (7.3)	78.5 (3.7)	59.0 (5.1)	15.8 (1.8)
	35 ♀	36.8 (2.1)	284 (15)	58.2 (3.4)	118.9 (7.8)	76.7 (3.4)	56.0 (3.7)	17.7 (1.6)
<i>mensurum</i>	8 ♂	41.1 (1.1)	312 (10)	59.4 (3.1)	126.6 (4.7)	79.9 (4.3)	57.0 (1.9)	17.2 (1.8)
	1 ♀	37.8	291	56.7	126.3	83.5	54.1	17.7
<i>infans</i>	2 ♂	37.0	277	54.0	115.5	84.0	56.0	15.5
	2 ♀	37.0	244	52.2	110.5	82.8	55.0	15.0
<i>macropus</i>	2 ♂	37.8	354	61.6	139.0	79.8	60.9	19.4
<i>slateri</i> (1)	10 ♂	37.8 (1.8)	306 (11)	60.5 (2.5)	122.9 (3.5)	78.0 (2.9)	54.7 (3.0)	17.2 (1.8)
	12 ♀	34.5 (2.1)	272 (16)	55.2 (2.9)	114.0 (4.8)	79.5 (2.9)	57.2 (3.6)	19.2 (1.7)
<i>slateri</i> (2) ...	8 ♂	38.9 (1.8)	317 (6)	59.3 (2.2)	120.7 (5.5)	75.9 (3.0)	55.8 (3.5)	16.8 (1.7)
	3 ♀	35.0 (2.4)	283 (8)	56.7 (3.1)	112.3 (6.4)	80.3 (4.5)	56.8 (3.9)	17.3 (1.7)
<i>graffi</i>	20 ♂	41.4 (2.1)	335 (21)	62.6 (2.9)	129.0 (4.8)	79.0 (4.2)	57.4 (3.8)	17.4 (1.6)
	11 ♀	39.2 (2.0)	303 (11)	60.1 (2.0)	120.4 (5.7)	76.1 (3.0)	54.4 (2.2)	18.2 (1.6)
<i>rufescens</i>	6*	38.2	316	61.1	127.8	75.3	49.3	16.7

* Entire Series.

† Includes jowls, which masks the relative narrowing of skull in maturing males of *A. c. caudicinctus*.

(1) Hermannsburg Series.

(2) George Gill Range Series.

Amphibolurus caudicinctus caudicinctus (Günther)

Grammatophora caudicincta Günther, 1875, in Richardson & Gray's "Zoology of the Erebus and Terror" 2: 19. Nickol Bay, Western Australia (F. H. du Boulay).

Amphibolurus imbricatus Peters, 1877, Mber. Preuss. Akad. Wiss. 1876: 529. Mermaid Strait, Western Australia (SMS "Gazelle").

Distribution.—Pilbara region of Western Australia from the De Grey River south to the Hamersley, Ophthalmia and Robertson Ranges. Also on Depuch Island, Dolphin Island (Dampier Archipelago), Monte Bello Islands (*vide* Hill 1955), and Barrow Island.

Description.—Juveniles dorsally reddish brown, dotted with black or dark brown. Two longitudinal series of dark spots arranged in pairs, one on each side of midline. Usually greyish white lines across body and tail alternating with dark paravertebral spots. Underneath whitish except for throat which may be flecked or dappled with grey.

As females mature, transverse whitish lines disappear from back, and dark spaces between pale caudal rings contract to form brown bars. Paravertebral spots become paler and usually disappear.

As males mature, tail and (to smaller extent) body become laterally compressed, head narrows and deepens, fleshy jowls develop about posterior corner of jaw, and throat swells. Head and back dull blood-red, colouring on flanks tending to concentrate in three wavy longitudinal streaks. Rump and upper surface of limbs olive grey. Tail yellowish brown (darker proximally), completely or almost completely encircled by blackish brown bands much narrower than pale

interspaces. Underneath whitish except for black patch on chest and grey marblings on throat.

Upper labials 12-19 (15.4). Lamellae under fourth toe 21-32 (27.2). Femoral and preanal pores 23-40 (31.5). Maximum SVL: Males 89, females 74.

Remarks.—In coloration and habitus adult males of this race diverge from juveniles and females to a much greater extent than in other races. Consequently workers with scanty material have understandably failed to identify *imbricatus* (based on juvenile) with *caudicinctus* (based on adult male), even though their type-localities are only 20 miles apart.

Another thing that has delayed the laying of the *imbricatus* ghost is that workers have referred to Boulenger's (1885 : 382) description of a South Australian "*imbricatus*" rather than to the original description. The notion thus arose that *imbricatus* was the eastern representative of *caudicinctus*. In other quarters "*imbricatus*" has been applied to juveniles generally.

Material.—Western Australia: North-West Division: R 2121 (De Grey); R 9867 (Strelley); R 19423 (Roebourne); R 17021, 17052-3 (Nickol Bay); R 19424-6 (Karratha); R 19378-82, 19427-8 (Erramurra Creek); R 13874 (Andover); R 13875 (Lilley B. Mine, via Roebourne); R 19432-42, 20205, 20207-11, 20218, 20221, 20225 (Mt. Herbert); R 19430-1 (Daniels Well); R 19443-57, 20228-9 (Millstream); R 20213, 20233 (Kangiangi); R 20227, 20231 (Mt. Ulric); R 19458-61 (21 mi. W of Tambrey); R 20216, 20220 (Pindrina Waters, 20 mi. NW of Tambrey); R 20212, 20219, 20224 (Tambrey); R 20206, 20214-5 (Tanberry Creek); R 10810 (Hooley);

R 19463 (16 mi. NW of Wittenoom); R 20217, 20222-3, 20226, 20230, 20232 (Asbestos Creek); R 13997 (Wittenoom); R 19465-6 (Yampire Gorge); R 13138, 19467-79 (Dales Gorge); R 13315, 13424, 19422 (Woodstock); R 10797-800 (Abydos); R 19410-21 (Marble Bar); R 11339 (Limestone); R 19388-409 (Mt. Edgar); R 19386-7 (Meentheena); R 14586-7 (Braeside); R 13254, 13259 (Mosquito Creek); R 13168 (Nullagine); R 19481 (14 mi. N of Roy Hill); R 19480 (17 mi. E of Marillana); R 17688, 25133-4 (Turee Creek); R 23985-6 (Mt. Newman); R 24012-4 (25 mi. NW of Mundiwindi); R 13338-9, 13603, 25210 (Jigalong). Eastern Division: R 25180-3 (20 mi. E of Jigalong). Islands off North-West Coast: R 14548-9, 14551, 14554, 14560-2 (Depuch); R 14252, 14280-3, 14293-5, 14299, 14328 (Dolphin); R 12890-1, 12893 (Barrow).

Amphibolurus caudicinctus mensarum
subsp. nov.

Holotype.—R 19486 in Western Australian Museum, an adult male collected by G. M. Storr on February 2, 1961, 5 miles south of Meekatharra, Western Australia, in 26° 40'S, 118° 27'E.

Distribution.—Murchison and East Murchison Goldfields of Western Australia from Mileura east to Mt. Fisher.

Description.—Head of adult male not so narrow or pointed as in nominate race and jowls less developed. Throat not swollen. Body depressed. Only distal part of tail compressed. Dorsal coloration duller, i.e. pale reddish brown. Caudal bands paler (i.e. brown) and not extending to lower surface. Hind-legs reddish brown, banded with olive or dark brown.

Females and juveniles differ from those of nominate race mainly in having larger, darker and more numerous dorsal spots (paravertebral series narrowly separated, adjacent spots occasionally coalescing to form short transverse bars).

Upper labials 12-17 (15.5). Lamellae under fourth toe 21-30 (25.2). Femoral and preanal pores 28-37 (33.6). Maximum SVL: males 81; females 62.

Remarks.—As discussed later under populations *incertae sedis*, this race intergrades with typical *caudicinctus*. If a boundary can be defined between them, it will probably be found to lie along the Ashburton River and Ilgararri Creek.

Paratypes.—Western Australia; North-West Division: R 15754, 15771-2, 15790-4 (Mileura); R 19482-5 (14 mi. N of Meekatharra). Eastern Division: R 21115-8 (Wiluna); R 13700 (Mt. Fisher, 110 mi. E of Wiluna).

Amphibolurus caudicinctus infans
subsp. nov.

Holotype.—R 25945 in Western Australian Museum, an adult male collected by G. M. Storr and W. H. Butler on November 7, 1965, at Deeba Rock-hole, 25 miles north-east of Laverton, Western Australia, in 28°22'S, 122°35'E.

Distribution.—Mt. Margaret Goldfield of Western Australia from Laverton south-west to Kookynie.

Description.—Considerably smaller than *mensarum*, with appendages relatively shorter and adult coloration scarcely different from juvenile.

Adult male: Head relatively short and broad; no jowls. Body slightly depressed. Tail not compressed. Dorsally reddish brown (with paler and duller vertebral streak); dotted with black, especially on head. Blackish longitudinally elongate paravertebral spots alternating with transverse rows of small pale pinkish brown or pinkish white spots. Lateral and dorsolateral surface with black and dark brown variegations including a dorsolateral series of crescentic spots. Ventrolateral surface of abdomen suffused with mustard-yellow. Hind-leg and base of tail obscurely and narrowly banded with greyish black. Remainder of tail broadly barred with dark greyish brown, 3-4 times as wide as pale interspaces. Lower lips vertically barred with dark grey. Throat dappled with grey. Black pectoral patch long and narrow, extending acutely on to abdomen, whence it continues as a grey streak to vent. Lower surface of distal segments of limbs dark grey. *Juvenile and adult female*: Body strongly depressed. Dorsally brick-red or orange brown, dotted with black or dark brown. Small, elongate, dark-brown paravertebral spots, forming on tail a single series. Pale transverse lines well developed on back and tail. Vertebral streak pale. Lips vertically barred with pale grey. Throat variegated with grey.

Nuchal crest very weak. Vertebrae scarcely differentiated from other dorsal scales. Dorsal keels strong, mucronate to subspinose. Upper labials 13-17 (14.3). Lamellae under fourth toe 22-25 (24.0). Femoral and preanal pores 32-42 (37.3). Maximum SVL: males 67, females 59.5.

Paratypes.—Western Australia; Eastern Division: R 25946-8 (25 mi. NE of Laverton); R 22583-4 (Mt. Morgans); R 15725, 22588-9, 25911 (Niagara Dam, 7 mi. SW of Kookynie).

Amphibolurus caudicinctus graafi subsp. nov.

Holotype.—R 25914 in Western Australian Museum, an adult male collected by G. M. Storr and W. H. Butler on November 4, 1965, at Mt. Eveline, Western Australia, in 26°10'S, 127°06'E.

Distribution.—Hills and granite outcrops of far eastern interior of Western Australia, from Warburton Range east to Barrow Range.

Description.—*Adult male*: Body depressed. Base of tail subcircular in section, slightly flattened on top. Dorsally dull yellowish brown (reddish in preservative). Dark paravertebral spots persistent only in smallest specimens. Legs and base of tail unbanded. Distal three-quarters of tail obscurely barred with dark greyish brown, more than twice as wide as pale interspaces. Flanks and dorsolateral surface of body dark grey (except for indistinct pale dorsolateral stripe in some specimens). Black pectoral patch larger than in other races (except *macropus*), narrowly extending on to anterior part of abdomen and often on to lower surface of arm. Throat with or without pale grey

variegation or obscure reticulum. Vicinity of gular fold suffused with salmon pink. *Adult female*: Dorsally reddish brown (brighter than male), flecked with blackish brown. Two rows of blackish brown paravertebral spots not widely separated and not well-aligned transversely. Occasionally a dorsolateral series of smaller spots. Scarcely any trace of transverse rows of pale dots.

Nasal on swollen rostral ridge. Keels of dorsal scales obtuse, weak to moderately strong, mucronate, concolorous with rest of scale. Ventrals smooth, sometimes feebly keeled on chest of males. Upper labials 14-20 (16.4). Lamellae under fourth toe 25-30 (27.2). Femoral and preanal pores 29-39 (34.6). Maximum SVL: males 79, females 72.

Remarks.—This race is named after Mr. Mark de Graaf, an Honorary Associate of this Museum, who collected many reptiles during his term as headmaster of the Warburton Range school. The local aboriginal name for this lizard is "tantalka" (M. de Graaf).

Paratypes.—Western Australia; Eastern Division: R 21999 (Granite Spring, 18 mi. NE of Warburton Range Mission); R 22037, 22195-6 (Windarro Spring, 1 mi. E of Granite Spring); R 19488, 25915-38 (Mt. Eveline, 38 mi. E of Warburton Range); R 15716-7 (13 mi. NE of Mt. Eveline).

Amphibolurus caudicinctus rufescens

Stirling and Zietz

Amphibolurus rufescens Stirling & Zietz, 1893. Trans. Roy. Soc. S. Aust. 16: 164. Mt. Sir Thomas, Birksgate Range, South Australia (Elder Expedition).

Distribution.—Far north-west of South Australia, south to the Birksgate Range and east to Granite Downs.

Description.—Head and body depressed. Tail proximally circular in section or flattened on top, slightly compressed distally. Nasal below relatively acute rostral ridge in adults; on swollen rostral ridge in single juvenile. Nuchal crest very weak in juvenile, stronger in adults. Dorsals small, keels weak and obtuse. Keels of laterodorsals reduced to small tubercles. Vertebral scales scarcely distinguishable from adjacent dorsals and thus not forming vertebral ridge. Spines above, behind and below ear strongly developed. Gulars weakly tuberculate and ventrals weakly keeled in juvenile; smooth in adults.

Upper labials 15-17 (15.3). Lamellae under fourth toe 26-33 (29.0), spines not dark. Femoral and preanal pores 32-62 (mean 53.2, but only the juvenile has less than 45). Maximum SVL 92, but Zietz (1915) measured 97mm in a specimen from Wantapella (5 mi. SW of Granite Downs HS.).

Dorsally "rusty-brown" (Stirling & Zietz). Series of dark spots on each side of midline, narrowly separate; spots may be circular, longitudinally elongate, or coalescing into wavy stripe of irregular width. Dark dorsolateral markings (dashes or crescents) orientated longitudinally and tending to coalesce. Vertebral and dorsolateral spots transversely elongate

on base of tail and tending to coalesce into narrow, widely separate, ill-defined bars. Distal half of tail faintly barred with dark brown. Upper surface of limbs obscurely and irregularly barred with brownish black blotches. Throat marbled with dark grey. Male pectoral patch "olive", extending narrowly on to abdomen and sometimes on to anteroventral surface of arm.

Remarks.—It is with some diffidence that I treat *rufescens* as a race of *caudicinctus*; for the scanty material is old or poorly preserved and, coming from widely separate localities, is highly variable. My main reasons for doing so are that *rufescens* is clearly a representative of *caudicinctus* and differs from other representatives in only two important respects; the numerous pores and the nostril located well below the sharp rostral ridge; but even these "key characters" are lacking in the single juvenile (SAM 1425).

With its weak nuchal crest and dorsal keels and in the colour pattern of the flanks, base of tail and upper surface of legs, *rufescens* shows some resemblance to *infans* from the other side of the Great Victoria Desert. The tendency for dorsal keels to be black points to the Central Australian populations. But apart from its long appendages, *rufescens* shows little resemblance to its nearest neighbour, *graeffi*. The systematic status of *rufescens* will thus remain in some doubt until the Cavenagh, Blackstone and Tomkinson Ranges are worked.

Material.—South Australia: SAM 1423 (holotype) and 1424-5 (paratypes) (Mt. Sir Thomas); SAM 5632 (Mann Range); SAM 586 (2 specimens, Everard Range).

Amphibolurus caudicinctus slateri subsp. nov.

Holotype.—R 26793 in the Western Australian Museum (formerly NTM 1471), an adult male collected by K. R. Slater on February 11, 1964, at Hermannsburg, Northern Territory, in 23° 58' S, 132° 46' E.

Distribution.—Southern highlands of the Northern Territory from the eastern Macdonnell Ranges south-west to the George Gill Range.

Description.—*Adult male*: Dorsally dull fawn, vaguely and narrowly banded with pale brown on distal (and occasionally proximal) part of tail. Small dark paravertebral spots occasionally persistent. Head and flanks obscurely variegated with dark grey and often dotted sparsely with brownish white. Throat usually dappled with grey. Subtriangular patch on chest bluish or blackish grey. Slight rosy flush occasionally discernible behind pectoral patch.

Adult female: Dorsally pale, dull reddish brown (somewhat paler and brighter than in male), finely dotted with black. Paravertebral spots small, dark brown, the two series widely separate. Whitish dots may be present on back (especially dorsolaterally), usually without definite arrangement, occasionally in transverse rows. Throat dappled with dark grey.

Body depressed. Tail not compressed. Nasal immediately below obtuse rostral ridge. Keels of dorsal scales black, strong, sharp, terminating in spine. Ventrals smooth. Upper labials

12-17 (14.6). Lamellae under fourth toe 24-32 (28.0). Femoral and preanal pores 27-39 (32.0). Maximum SVL: males 83, females 69.

Geographic variation.—Coloration of the adult male, as given above, is based on topotypical material. In the George Gill Range, males differ in having (1) dorsum somewhat reddish on occiput, nape, arms and anterior part of back, (2) flanks obscurely variegated with dark brown, and (3) lower surface of arm and immediately behind gular fold orange-yellow. Specimens from George Gill Range also differ in their longer head and tail (see Table 1) and more numerous subdigital lamellae (averaging 28.6 under fourth toe, against 27.5 at Hermannsburg).

Remarks.—With its reduced sexual dimorphism, plain coloration and short appendages, *slateri* is very different from nominate *caudicinctus*. It is not surprising, then, that workers have had difficulty in placing Central Australian members of the species.

Specimens collected by the Horn Expedition at Alice Springs, Finke Gorge and Charlotte Waters were referred by Lucas & Frost (1896 : 126) to *A. imbricatus*. They pointed out discrepancies in coloration and number of pores between their specimens and Peters' original description.

Sternfeld (1924) had five specimens from Hermannsburg which he tentatively placed with *caudicinctus*. He was aware of their difference from typical *caudicinctus* in caudal coloration and length of limbs. Sternfeld drew attention to errors in Boulenger's (1885 : 384) description of *caudicinctus* and correctly prophesied that the species would prove divisible into several races.

Loveridge (1934 : 319) had a single specimen from Hermannsburg and, following Sternfeld, referred it (with specimens of *mensarum*) to *caudicinctus*, even though they keyed out to *imbricatus*. He suggested that *imbricatus* and *rufescens* were races of *caudicinctus*.

This race is named after Mr. K. R. Slater, in appreciation of the many courtesies he extended to the Western Australian Museum during his sojourn at Alice Springs. Mr. Slater kindly donated the holotype to this Museum.

Paratypes.—Northern Territory: SAM 3581 (between Alice Springs and Hart Range); R 20902 (Alice Springs); R 20869, NTM 1472-5, NTM 2379-96 (Hermannsburg); NTM 2378 (Palm Valley); NTM 2018-9 (Kathleen Creek, George Gill Range); NTM 1943, NTM 2670-9 (Reedy Creek, 6 mi. W of Kathleen Creek).

Amphibolurus caudicinctus macropus
subsp. nov.

Holotype.—R 3229 in the South Australian Museum, an adult male collected by R. R. Miller (American-Australian Arnhem Land Expedition) on September 30, 1948, 4½ miles south-southeast of Oenpelli, Northern Territory, in 12°23'S, 133°05'E.

Distribution.—North-western edge of Arnhem Land plateau, Northern Territory.

Description (of adult male).—Dorsally dull reddish brown with or without two widely separate series of small dark-brown paravertebral spots. Tail yellowish brown, banded on top and sides with dark brown; proximal bands ill defined, narrower than pale interspaces; distal bands darker and better defined. Black pectoral patch covering entire width of chest, beginning on gular fold and extending squarely back on to anterior part of abdomen (and in one specimen on fore-arm).

Much larger than other races (except *rufescens*), with relatively longer tail and hind-leg (see Table 1). Distal three-quarters of tail compressed. Nasal small, located on top of obtuse rostral ridge. Keels of dorsal scales moderately strong and sharp, terminating in mucron or short spine. Ventrals weakly keeled. Upper labials 15-16. Lamellae under fourth toe 31-35. Femoral and preanal pores 29-31. SVL: holotype 89, paratype 101.

Remarks.—In its great size, large pectoral patch, weakly spinose dorsal scales and compressed distal part of tail, *macropus* unexpectedly resembles *rufescens* from a thousand miles to the south.

Paratype.—USNM 128751 (same data as holotype).

Incertae sedis

Several collections made in winter contain only juveniles and subadults. While they are not identifiable to subspecies, these series help to fill out the range of the species and are listed below together with any data that indicate their systematic affinities.

1. *Ashburton, upper Gascoyne and Ilgararri Creek drainages (W.A.):* R 13923 (2 specimens from 10 mi. N of Mt. Wall); R 15819 (21 mi. NNW of Ullawarra); R 19429 (Barlee Range); R 22823 (18 mi. NW of Mt. Vernon HS.); R 25240 (foot of Mt. Vernon); R 22697 ("Mulgul or Mt. Vernen"); R 23997 (Kumarina); R 23933-4 (20 mi. NW of Beyonde); R 15843-4 (Weld Spring, Canning Stock Route); R 15839 (17 mi. N of Weld Spring).

The largest of these specimens, R 22697, is a male with SVL 74 mm. The base of its tail is slightly compressed, the legs are banded, and it retains paravertebral spots. It is thus an intergrade between *caudicinctus* and *mensarum*, but nearer to the latter. In contrast, a much younger male (SVL 61) from Turee Creek (50-80 miles further north and across the Ashburton) is indistinguishable from typical *caudicinctus*. In the larger (SVL 49.5) of two juveniles from near Mt. Wall (likewise north of the Ashburton) the tail is already beginning to compress; it is therefore likely that this population belongs to the nominate race, which is also to be expected on geographic grounds (Mt. Wall being a south-western outlier of the Hamersley Ranges). The young males from Beyonde resemble *mensarum* more than *caudicinctus*. The three juveniles from the Canning Stock Route are very reddish, like juveniles of *mensarum* from Wiluna.

- CAUDICINCTUS
- ▲ MENSARUM
- INFANS
- X GRAAFI
- RUFESCENS
- ▼ SLATERI
- MACROPUS

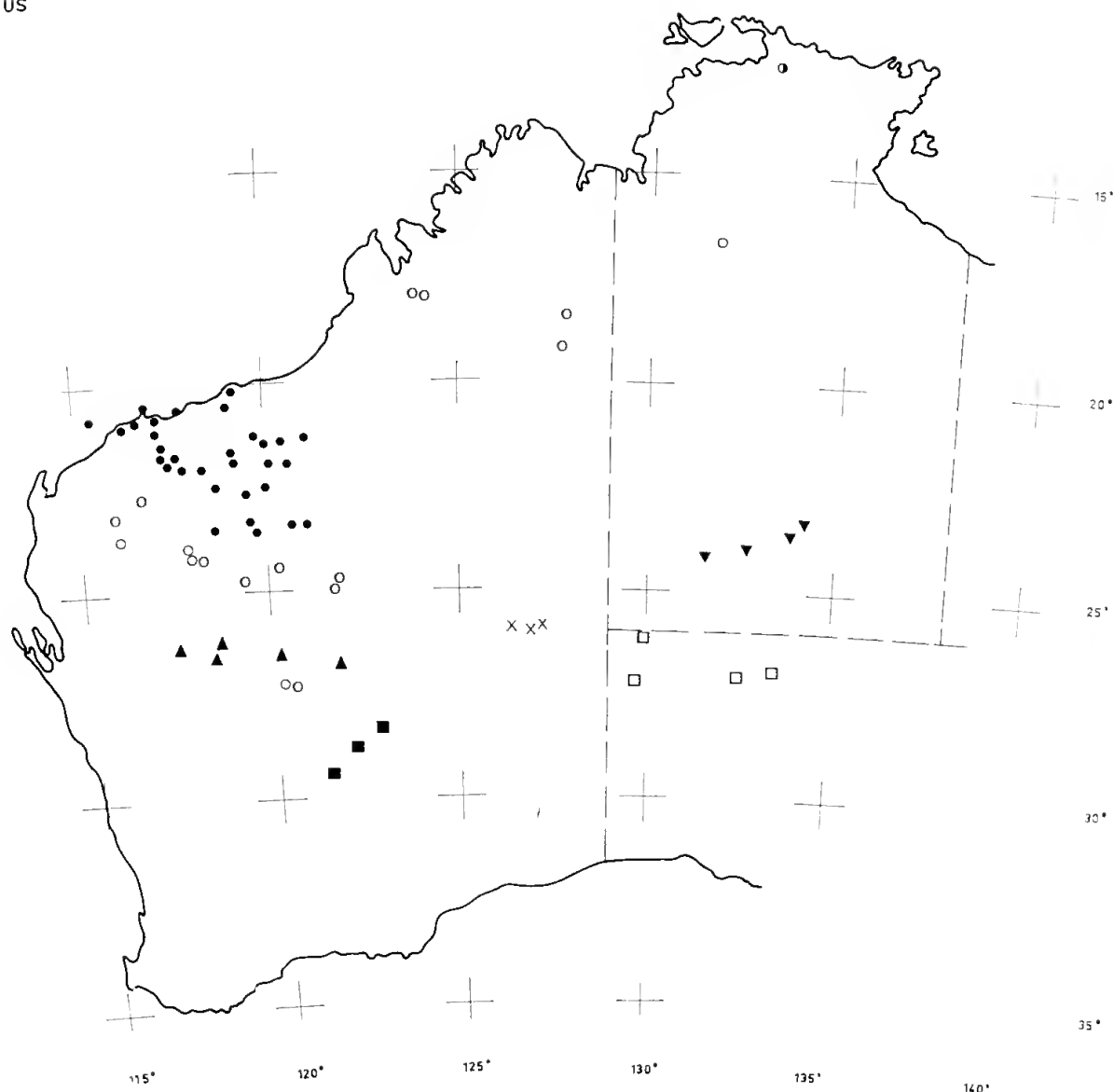


Figure 1.—Map of Western Australia, Northern Territory and north-western South Australia, showing location of specimens of subspecies of *Amphibolurus caudicinctus*. Specimens unidentified to subspecies are located by hollow circles.

2. *Barr Smith Range* (W.A.): R 19783 (Albion Downs); R 19487 (19 mi. NE of Kathleen Valley). The latter has an egg in the ovary. Though as large as a gravid *mensarum*, this specimen has a much shorter head and tail, in which respect it agrees with female *infans*.

3. *Victoria River drainage* (N.T.): R 13721 (Top Springs). This young male (SVL 61) is surprisingly similar to *slateri*, even to the strong black keels of the dorsal scales. Relative length of appendages is just within the upper limits of *slateri*. Its ventral scales are weakly keeled, a feature shared with *macropus* from 300 miles further north.

4. *Southern interior of Kimberley Division* (W.A.): R 26794 (Mt. Anderson); R 23032 (Grant Range, 3 mi. NW of Liveringa); R 23056-7 (20 mi. SE of Halls Creek); SAM 3573 (3 specimens from Wolf Creek).

Only R 26794 is fully adult—a female (SVL 72) collected in late May. It has a longer tail (316% of trunk) than any female of nominate race and a larger ear-aperture (20% of head-length) than all females of nominate race with

SVL greater than 63. Its dorsal coloration is dull reddish brown; the paravertebral spots are well developed anteriorly, but on posterior half of back they break up into transverse rows of small spots; also posteriorly the transverse rows of whitish spots persist.

The remaining specimens were collected in September, the largest (SVL 62.5) being a young male with blackish-grey pectoral patch. Their upper surface is uniformly pale brown, dotted finely with black; the paravertebral spots are small. In coloration they are thus similar to *slateri*, but disagree in their relatively long appendages and weak keeling of dorsal scales. The last feature also separates them from the specimen from Top Springs (300 mi. ENE of Halls Creek).

Ecology

Habitat

A. c. caudicinctus is widespread and abundant in the Pilbara, a region in which precipitous hills, razor-backed ridges of dolerite and piles of granite and other crystalline rocks are sel-

dom out of view. In most of this country *caudicinctus* is not only the commonest agamid, but few others are encountered apart from *Physignathus longirostris* which is largely restricted to wooded watercourses. It is only on the coastal plains and in some of the broader river valleys that *caudicinctus* becomes scarce or absent and other agamids (especially *Amphibolurus inermis* and *A. isolepis*) are plentiful. *A. c. caudicinctus* is not confined to rocky areas but may be found on plains of spinifex (*Triodia*) in the valley of the Fortescue, though generally only on heavy, stony soils shunned by *inermis* and *isolepis*. Here it occurs with *Amphibolurus reticulatus*, which however is scarce in this (the northernmost) part of its range.

South and south-east of the Ashburton River mountain ranges are fewer and widely separated. Here the undulating Precambrian Shield is not greatly dissected, and relief is provided mainly by buttes, mesas and "breakaways" (i.e. low cliffs leading up to minor plateaux). The vegetation is mulga scrub, which is notably deficient in ground cover. Suitable conditions for *A. c. mensarum* and *infans* are thus generally not plentiful or continuous, and moreover they must compete with increasing numbers of other agamids. *A. reticulatus* is common in stony areas, and *A. scutellatus*, *cristatus* and *ornatus* find their northern limits within the range of *mensarum*.

No form of *caudicinctus* has been collected in the eastern deserts of Western Australia, even though belts of residual sandstone commonly rise above the extensive areas of sand dunes. On the northern edge of the Great Victoria Desert, *A. c. graafi* shares with *Tympanocryptis lineata centralis* rocky habitats in the Warburton and Townsend Ranges. Further east it is replaced by *A. c. rufescens* which evidently occupies all the granitic hills of far northern South Australia. The several mountain ranges of Central Australia are usually separated by sandy lowlands unsuitable for the species. The resultant archipelagic kind of distribution lends itself to subspeciation the full extent of which will not be appreciated until all these mountains are explored.

The highlands of the Kimberley Division, the watershed between the Victoria and Daly Rivers and the sandstone plateaux of Arnhem Land and the McArthur River are virtually *terra incognita* as far as their reptiles are concerned. They could well harbour abundant and diverse populations of *Amphibolurus caudicinctus*.

Breeding Season and Longevity

The precise date of collection is known for 165 individuals of our large series of *A. c. caudicinctus*. These break down by month, age and sex as follows. Range in snout-vent length is given in brackets.

February: 3 adult males (76-84); 7 adult females (62-70), all gravid except one (the largest).

March: 13 adult males (68-86); 23 adult females (57-72), all but five gravid; subadult male (65); 3 juveniles (25-48).

April: 4 adult males (77-83); 1 adult non-gravid female (74); 1 juvenile (25).

May: 2 adult males (81-89); 2 adult non-gravid females (61-63); 12 juveniles (23-46).

June: 1 adult male (80); 1 adult non-gravid female (70); 13 juveniles (28-50).

July: 2 subadult males (60-73); 17 juveniles (31-52).

August: 13 subadult males (56-68); 31 juveniles and subadult females (37-58).

September: 1 juvenile (56).

October: 1 adult male (75); 3 adult non-gravid females (59-69); 1 subadult male (62); 1 juvenile (55).

November: 3 adult males (71-80); 1 gravid female (67).

December: 2 adult males (75-76); 1 adult female (60); 1 juvenile (54).

Because the breeding season lasts for at least five months, it is not so easy to analyse the above data as was done elsewhere for the *Amphibolurus maculatus* species-group (Storr 1965). Nevertheless it seems fairly certain that *A. c. caudicinctus* breeds at about nine months of age and dies a few months later.

The eggs evidently hatch between January and May. Males begin to acquire adult characteristics (at SVL about 55) between June and September, mature between October and March, breed and continue to grow till the last of them die in early June. Females are gravid between November and March, continue to grow after laying, the last of them disappearing in early June.

Ecological effects on morphology

The races of *A. caudicinctus* can be compared with respect to relative length of appendages in Table 1 and better still in Table 2, which gives percentage departures from normal. "Normal" was obtained by averaging for each appendage the mean relative length in adult males of each race. Also given in Table 2 are mean latitude and mean annual temperature.

It will be seen that Allen's Rule (that appendages are relatively longer in warmer areas) is only partly followed here. Agreement is perfect in the series *caudicinctus*—*mensarum*—*infans*; but these are the only races that are contiguous and intergrading. Among the isolated eastern races there are numerous anomalies: the short head of *macropus*, the long head and tail of *graafi*, the short head and tail of topotypical *slateri* (compared to those of George Gill Range lizards), and the long appendages of *rufescens*.

Elsewhere it was established for the *Amphibolurus maculatus* and *reticulatus* species-groups (Storr 1965, 1966) that with decreasing temperature the number of upper labials increases and the number of subdigital lamellae decreases. Table 2 shows that the first of these generalisations does not hold here; on the contrary, labial counts are generally higher in warmer regions. The second generalisation does hold in the present species. In the western sequence, *caudicinctus*—*mensarum*—*infans*, lamellar counts steadily decline. In the eastern races counts are generally higher, but in *graafi* and topotypical *slateri* they are anomalously low.

TABLE 2

Mean latitude ($^{\circ}$ S), mean annual temperature ($^{\circ}$ F) and deviation (%) from normal in mean relative length of appendages of adult males and in mean number of upper labials and lamellae under fourth toe.

	Latitude	Annual Temperature	Relative Length of				Number of	
			Head	Tail	Foreleg	Hindleg	Labials	Lamellae
Western—								
<i>caudicinctus</i>	21.9	77	+ 6	+ 1	+ 3	+ 1	+ 1	— 2
<i>mensarum</i>	26.4	72	+ 5	— 2	— 1	0	+ 2	— 9
<i>infans</i>	28.9	68	— 6	— 13	— 10	— 8	— 6	— 13
Eastern—								
<i>macropus</i>	12.4	82	— 4	+ 12	+ 2	+ 10	+ 2	+ 20
<i>slateri</i> (1)	24.0	70	— 4	— 4	+ 1	— 2	— 4	— 1
<i>slateri</i> (2)	24.3	69	— 1	0	— 1	— 4	— 3	+ 3
<i>graffi</i>	26.6	71	+ 6	+ 6	+ 4	+ 2	+ 8	— 2
<i>rufescens</i>	26.8	69	— 3	0	+ 2	+ 1	0	+ 5

(1) Hermannsburg Series.

(2) George Gill Range Series.

In the extreme depression of its head and body, *rufescens* approaches the south-western species *Amphibolurus ornatus*. It could well be that *rufescens*, like *ornatus*, is adapted for sheltering under slabs of exfoliated granite. At any rate it is closely associated with granitic rocks (White 1915).

At the opposite extreme to *rufescens* is adult male *caudicinctus*, whose compressed head, body and tail immediately separate it from all other races and cause it alone to resemble the arboreal agamids in habitus. Now adult males of the nominate race are commonly observed in the tops of shrubs and low trees, especially dead ones or on dead sticks. Almost certainly they are basking rather than feeding or taking refuge from predators. They quickly drop to the ground and seek terrestrial cover on the distant approach of an intruder, whereas the truly arboreal *Physignathus longirostris* is more likely to freeze or climb higher in the presence of man. No females or juveniles of *A. c. caudicinctus* have been observed in vegetation, nor any individual of other races.

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7.—A 3,300 year old Thylacine (Marsupialia: Thylacinidae) from the Nullarbor Plain, Western Australia

by Jeannette Partridge*

Manuscript received 21 February 1967; accepted 21 March 1967

Abstract

An almost complete skeleton of the thylacine, *Thylacinus cynocephalus* (Harris), was recovered from Murra-el-elevyn Cave on the Nullarbor Plain, Western Australia. Analysis of dried tissue attached to the bones gave a C^{14} date of $3,280 \pm 90$ years, making this specimen the youngest thylacine yet recovered from the mainland of Australia.

Introduction

In December 1963 and January 1964 members of the Sydney University Speleological Society organized an expedition to the Nullarbor Plain. During the exploration of the cave Murra-el-elevyn, near Cocklebidy in Western Australia, the remains of a thylacine were discovered by Mr. N. Campbell. Most of the skeleton was removed from the cave before it could be photographed *in situ*, and it proved impossible at the time to return and collect the remainder.

Murra-el-elevyn Cave, one of the deeper caves on the Nullarbor, is situated about five miles west of Cocklebidy Tank. The entrance to the cave is at the bottom of a deep undercut collapse doline. The cave consists of several large chambers of considerable depth, the water-level of the lake in the first chamber being about 289 feet below ground level (Anderson 1964). Lundelius (1963) collected from a limited area below the overhanging roof the remains of small mammals which he considered to be derived from regurgitated owl pellets. In contrast to this collection, the thylacine was found well inside the cave, lying in loose dry sand in an upper passage among the boulders of a rockfall. At the time the presence of the thylacine so far within the cave suggested the existence of a second entrance, but a short search failed to reveal one.

Description of the specimen

The thylacine skeleton (W. Aust. Mus. specimen 64-8-1) consists of the following: the complete skull and mandible with all teeth in place; the vertebral column with the exception of the sacrum and caudal vertebrae; nine ribs; the right half of the pectoral girdle and the right forelimb, and the left half of the pelvic girdle and left hindlimb. Many of the bones were still articulated and in several cases dried soft tissues were attached to them. The right humerus and clavicle were embedded in a sheet of this material (Fig. 1). Except for the atlas and the last lumbar vertebra, the backbone was recovered in three sections with the vertebrae

still articulated and partly covered with the dried tissue. The radius was joined to the fully articulated bones of the manus, which was also covered with dried tissue. The bones of the pes were similarly recovered as a unit.

The skeleton seems to be that of a mature thylacine. All the teeth have erupted and their occlusal surfaces show a mild degree of wear. None of the bones collected show any signs of premortem damage. One of the transverse processes of the last lumbar vertebra has been broken off, and some of the teeth are chipped, but this damage probably occurred during the removal of the skeleton from the cave. There is no evidence as to the cause of death.

TABLE 1

Comparison of the Murra-el-elevyn specimen with the Western Australian cave fossils of *Thylacinus cynocephalus*

Character	W.A.M. 64.8.1	Western cave thylacines (Ride 1964)	
	x mm.	x mm.	Range mm
M ² pr.-mc.	12.6	13.0	11.4-16.0
M ³ pr.-mc.	13.7	15.4	13.2-17.6
M ¹⁻⁴ length	38.3	40.0	36.8-45.9
P ₁ length	9.6	10.7	9.3-12.1
P ₁ C length	47.6	49.9	38.0-57.9
M ₁ length	13.0	14.9	12.8-16.9
Ht at P ₄	24.3	29.9	24.4-34.8

Ride (1964) compared the dental characters of thylacines from the cave faunas of both eastern and western Australia with the modern Tasmanian population of *Thylacinus cynocephalus* (Harris). He concluded that the size difference between the smaller western thylacines and the larger eastern forms, both fossil and modern, was not significant at a specific or subspecific level. Comparative dental measurements (Table 1) show that the thylacine from Murra-el-elevyn Cave falls at the lower end of the size range of *Thylacinus cynocephalus* from south-western Australia. This suggests that the skeleton is that of a female, there being a marked sexual dimorphism in *Thylacinus*.

Age

An estimation of the age of the skeleton was obtained by a carbon 14 assay of part of the dried tissue attached to the bones. This gave a direct date of the time of death of the thylacine on the Nullarbor at 3280 ± 90 years B.P.

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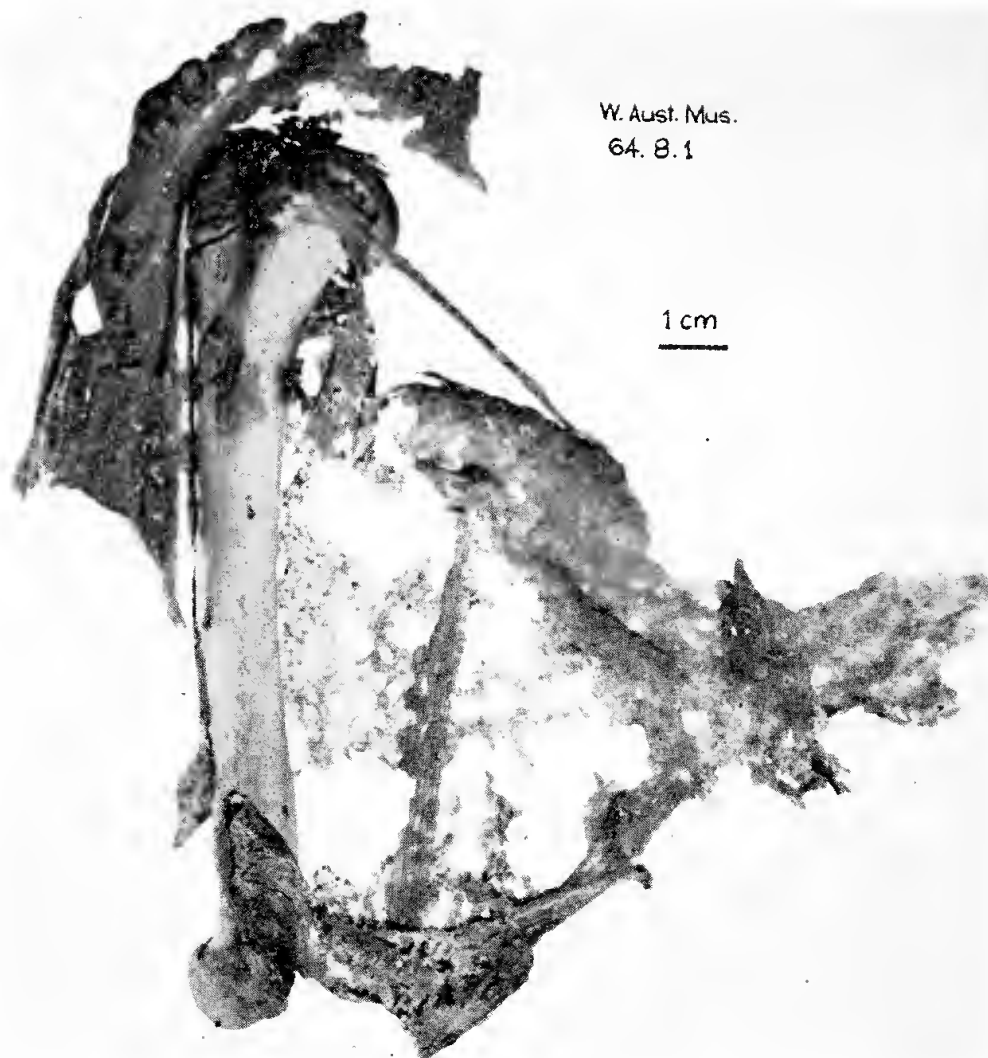


Figure 1.—Right humerus and clavicle of the Murra-el-elevyn thylacine showing attached dried tissue.

Discussion

The thylacine has existed in historical times only in Tasmania where it is now extremely rare and may be on the verge of extinction. Cave fossils indicate that it once ranged widely throughout mainland Australia. Two size forms are known, the smaller western Australian form, which includes the Murra-el-elevyn thylacine, and the larger eastern Australian form, which includes the historical Tasmanian population. The species is represented in New Guinea by a mandible from an archeological level dated at about 10,000 years B.P. (Van Deusen 1963, Bulmer 1964). The only other recent, genuinely dated specimen is a small, morphologically unusual, thylacine molar from an archeological excavation at Fromm's Landing on the Murray River in South Australia (Macintosh and Mahoney 1964). This was found at a level dated at 4,000 years B.P. The 3,300 year old thylacine from Murra-el-elevyn is thus the most recent specimen yet found.

The smaller western thylacine has been reported from bone deposits in many of the caves of south-western Australia (Glauert 1948, Cook 1963). The only other record from the Nullarbor Plain is of single thylacine molar associated with

remains of the Tasmanian devil, *Sarcophilus harrisi*, in Webb's Cave, Mundrabilla Station, Western Australia. (Cook 1963a). The widespread occurrence in Western Australian cave deposits of the thylacine and the Tasmanian devil, both now restricted to Tasmania, has led to the suggestion that they may be indicative of more humid climatic conditions in the past (Cook 1963) and that their present absence may be related to climatic change. If this is so, the presence of the thylacine on the Nullarbor as late as 3,300 years ago would suggest that at least until that time there was no essential climate change in the area. This supports Lundelius' (1960) findings that in the cave deposits of south-western Australia there is no evidence of a period between 4,000 and 7,000 years ago of greater aridity than at present, as has been suggested by Gill (1955) for Victoria.

However, it is possible that the thylacine is not a reliable indicator of climatic change, and that its extinction on the mainland cannot be attributed to increasing aridity alone. Other factors such as disease and competition with the dingo have been suggested as contributing to its decline. In this connection it is interesting to note that the oldest genuinely dated

dingo comes from a 3,000 year old level of the Fromm's Landing excavation (Macintosh 1964), and so approximately coincides in age with the Murra-el-elevyn thylacine.

Acknowledgements

I am indebted to the Speleological Research Council Ltd. whose grant covered the cost of the C^{14} estimation. This was carried out at the laboratory of Professor Kigoshi, Gakushuin University, Tokyo, Japan. I am particularly grateful to Mr. D. Merrilees of the Western Australian Museum for his advice, and to Mr. D. Gordon who photographed the specimen.

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8.—The vanadium-bearing magnetite gabbro* at Coates, Western Australia

by D. R. Hudson†

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Abstract

A recent investigation of the vanadium-bearing magnetite gabbro at Coates, Western Australia has made possible a study of unaltered rock samples from below the deep zone of lateritisation and kaolinisation. The association of oriented plagioclase tablets, abundant opaque oxides, cummingtonite and Na-hornblende is explained as an igneous differentiate from a gabbroic magma.

Analyses of the gabbro and its kaolinised equivalent indicate that vanadium has suffered only slight depletion during weathering. Laterites containing high concentrations of vanadium and titanium are derived from the gabbro by leaching and selective precipitation, but are of limited extent.

Vanadium is concentrated in the magnetite relative to the coexisting ilmenite, while manganese is preferentially accommodated in the ilmenite. The opaque oxides appear to be related to the titaniferous magnetite bodies occurring in central and northwestern Western Australia.

Introduction

Vanadium-bearing magnetite gabbros and associated laterites occur near Coates Siding, 45 miles by road east-north-east of Perth, Western Australia. The magnetite gabbro forms a prominent ridge extending northwest from Coates, with a probable minor extension 1.5 miles further to the north.

The gabbro has been extensively lateritised with almost complete destruction of the primary minerals. Original textural features, however, are generally well preserved and permit limited structural interpretation. Titanium-rich laterites occur high on the western flank of the ridge, while pisolitic laterites and lateritic soils occur on the eastern flank and on the western flank below the titanium-rich laterites. Granitic rocks outcrop to the east of the ridge and it is probable that the gabbro bears an intrusive relationship to them.

Early geological interest in the area centred on the possibility of exploiting the laterites as a source of iron for the nearby Wundowie charcoal-iron blast furnace (Connolly 1959). Several shallow prospecting pits were dug, both in the titanium-rich laterites and pisolitic laterites. The laterites, however, proved uneconomic to mine due to their sporadic distribution and undesirably high titanium content.

In 1961 interest was renewed in the laterites and the parent gabbro as a possible ore of vanadium. Mangore Australia Pty. Ltd., an Australian subsidiary of Union Carbide Corporation, carried out an extensive drilling and sampling programme, in the course of which a shaft was sunk to a depth of 101 feet in the

centre of the lateritised magnetite gabbro. The shaft encountered unaltered gabbro 90 feet below the surface (Fig.1). A summary of the vanadium ores investigated by Mangore Australia Pty. Ltd. is given by Jones (1965).

Magnetite gabbro

Occurrence

The magnetite gabbro occurs as a steeply dipping NW-trending dyke, apparently intrusive into granite. Lateritised gabbro can be traced along strike for at least one mile with an average width of 300 feet. Compositional banding is pronounced, with variation from anorthositic bands to solid magnetite lenses. The latter appear to be relatively narrow, usually not wider than 6 inches, and rarely extend further than a few feet along strike. Abundant magnetite boulders, however, indicate that these lenses are widespread. Paucity of outcrop prevents a systematic study of compositional variation in the gabbro, but both the magnetite lenses and anorthosites are concentrated on the eastern wall of the dyke.

Despite lateritisation a strong palimpsest igneous lamination can be observed throughout the dyke. The foliation, developed by alignment of tabular plagioclase crystals, strikes parallel to the trend of the dyke and indicates a vertical or steep easterly dip. This dip is confirmed by the lenticular magnetite bodies.

Ground magnetometer traverses (Fig.1) give a high positive anomaly over the full width of the gabbro and confirm the limits of outcrop deduced from surface exposure.

General petrography

Although abundant lateritised magnetite gabbro can be observed at the surface, the only fresh material available for study comes from the bottom of the shaft. Here the rock is green-black in colour and is composed of coarse, tabular plagioclase crystals. Magnetite grains are interstitial to the plagioclase and are rimmed by dark green amphibole (Fig. 2). Chlorite veinlets, many of them carrying sulphides, are common.

Plagioclase (58.6 per cent., by volume) occurs in subhedral grains of average size 5 x 4 x 1.5 mm, which are tabular parallel to (010). Most grains show combined Carlsbad and albite twinning with rarer combined pericline twinning. A clouded appearance is given to the grains by minute exsolution rods. Patchy alteration to sericite and kaolin is common, and is particularly well developed in the cores of grains where it is sometimes associated with zoisite. Extinction angles $X' \wedge (010)$, measured normal to a are

* The modal composition departs markedly from the range normally covered by the term gabbro, but it has been so named in previous published work and there seems to be no appropriate alternative.

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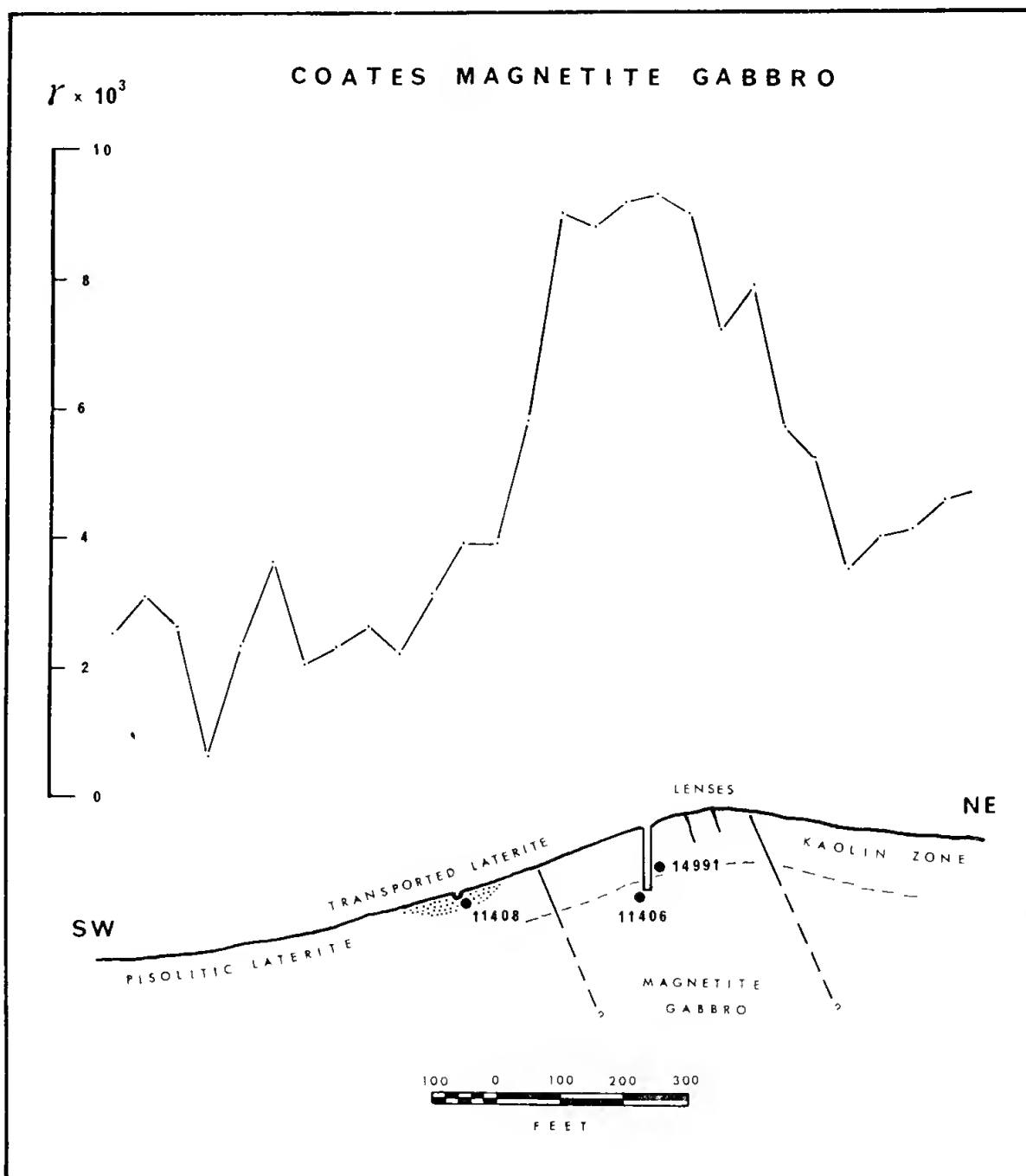


Figure 1.—Vertical section through Coates magnetite gabbro. (Numbers refer to specimens housed in the Department of Geology and Mineralogy, University of Queensland.)

$29^{\circ} \pm 2^{\circ}$, indicating labradorite, An_{54} . Post crystallisation fractures and plagioclase-plagioclase and plagioclase-magnetite grain boundaries have been filled and replaced by prismatic to granular aggregates of Na-hornblende.

Na-hornblende (15.4 per cent.) occurs dominantly as aggregates growing normal to grain boundary interfaces. Larger subhedral grains, up to 2 mm in diameter have grown by replacement of cummingtonite. The mineral is strongly pleochroic, with X = pale yellow, Y = deep green and Z = blue-green. Refractive index $\delta = 1.637 \pm 0.002$.

Cummingtonite (1.6 per cent.) remains as colourless grains of average size 1.5 x 1 mm, showing partial or complete reaction to Na-hornblende. Abundant, drop-like exsolution

particles (? magnetite) are arranged in rows parallel to (001) and (010). The mineral is optically positive with refractive index $\delta = 1.682 \pm 0.002$.

Biotite occurs as pale brown, pleochroic flakes intergrown with the Na-hornblende aggregates, while plumose chlorite fills veins cutting all other minerals.

Pyrite (0.3 per cent.) is associated with chlorite in small veinlets and also occurs as discrete granules throughout the rock.

Opaque oxides

The ore minerals are interstitial to the plagioclase tablets and form subcontinuous aggregates throughout the rock. Magnetite (20.1 per cent., by volume) is the dominant oxide and encloses smaller irregular grains of ilmenite (4.0 per

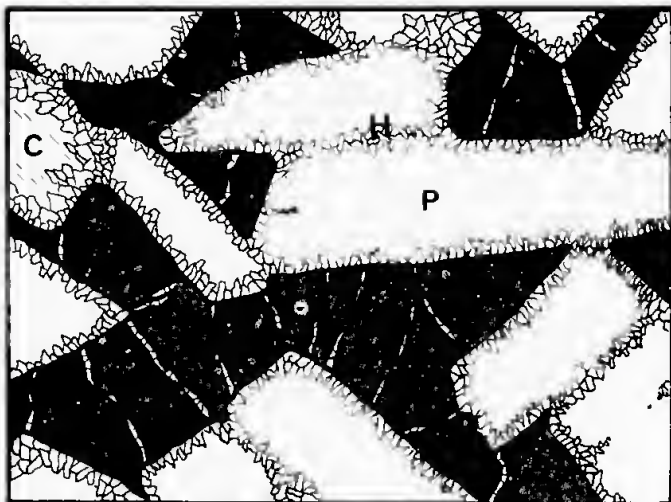


Figure 2.—Sketch of magnetite gabbro 11406, drawn from a thin-section. Width of field is 1 cm. Plagioclase (P), white; Na-hornblende (H), granular; cummingtonite (C); magnetite and ilmenite, black.

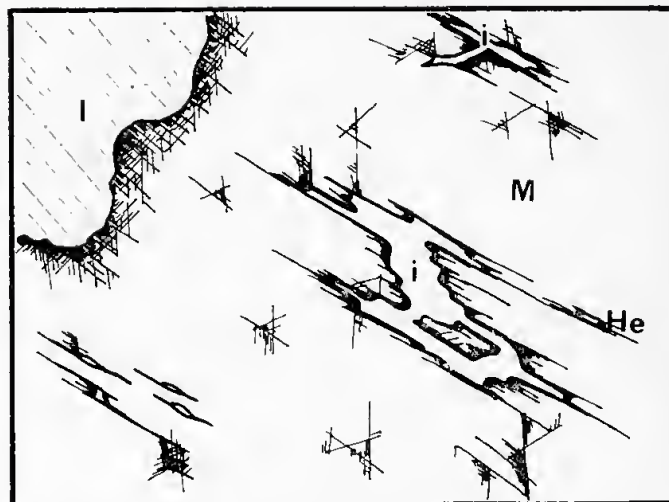


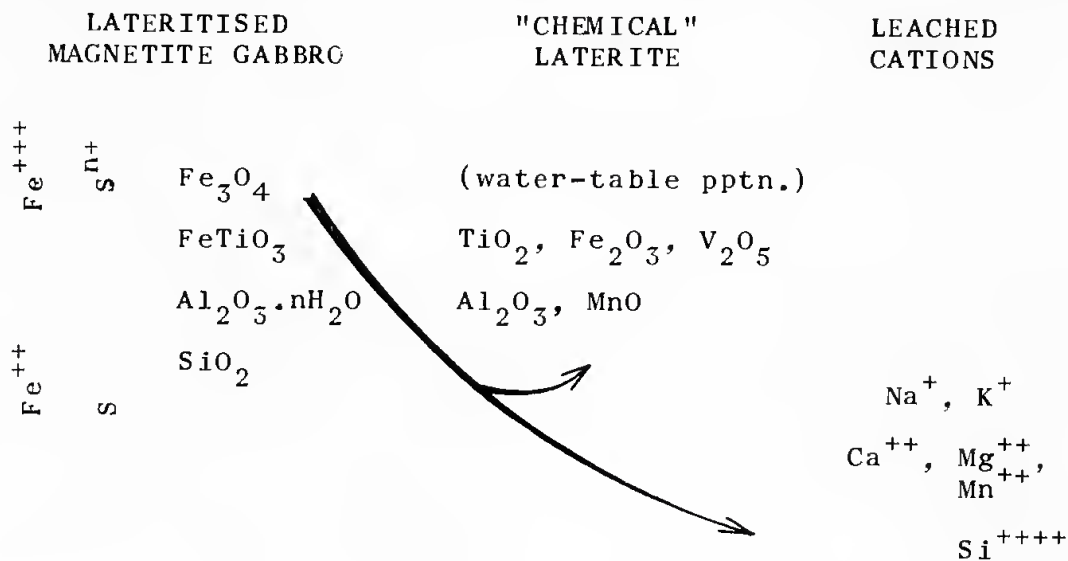
Figure 3.—Sketch of opaque oxides from gabbro 11406, drawn from a polished surface. Width of field is 1 mm. Magnetite (M), containing exsolved ilmenite (i); haematite (He), black; ilmenite (I).

cent.), most of which occur near the magnetite grain margin. The ilmenite grains rarely measure more than 1 mm in diameter and are usually much smaller. They are grey in colour and show marked anisotropism. Fine anisotropic lamellae ($10\ \mu$ in length and $1\ \mu$ in width) occur parallel to (0001) and are probably exsolved haematite (Fig. 3). Vincent and Phillips (1954) record similar exsolution lamellae in ilmenites from the Skaergaard intrusion, but consider them to be dominantly magnetite.

Magnetite is grey in colour and isotropic. It is difficult to polish and almost always shows irregular pitting. Under low power, plates and lamellae of ilmenite, most of which are in the

(111) planes of the magnetite, can be seen. The ilmenite has a much deeper purple tint than that occurring in discrete grains and contains no exsolved haematite. Under high power ($\times 400$) further ilmenite rods can be seen in triangular intergrowths with magnetite. Haematite occurs rimming exsolved ilmenite and as fine octahedrally controlled textures in the magnetite (Fig. 3). Replacement of magnetite by haematite is common along ilmenite-magnetite grain boundaries and along fractures.

The solid magnetite lenses outcropping in the lateritised portion of the gabbro (11407) are extensively altered to haematite. Coarse ilmenite lamellae are visible under low power, but discrete ilmenite grains are rare or absent.



Relative mineral stability: ILMENITE > MAGNETITE > amphiboles >
feldspars

Figure 4.—Relationship between residual and transported laterites, Cortes Siding.

TABLE 1
Chemical analyses of Coates magnetite gabbro
(Analyst: D. R. Hudson)

Weight per cent.	ROCKS			MINERALS	
	GABBRO 11406	KAOLINISED GABBRO 14991	LATERITE 11408	MAGNETITE 11406	ILMENITE 11406
SiO ₂	30.07	23.05	0.16	0.38	
TiO ₂	5.55	6.64	28.98	7.51	48.51
Al ₂ O ₃	14.87	18.74	6.93	2.58	
Fe ₂ O ₃	19.08	27.67	51.63	60.07	6.40
Cr ₂ O ₃	tr	tr	tr	nil	0.01
FeO	17.31	13.09	1.12	27.19	40.62
MnO	0.16	0.12	0.06	0.10	0.81
MgO	2.95	0.48		0.46	1.51
CaO	5.32	tr		0.02	0.22
Na ₂ O	1.58	0.18			
K ₂ O	0.31	0.17			
H ₂ O+	1.61	7.32	8.75		
H ₂ O-	0.08	1.77	0.72		
P ₂ O ₅	0.34				
V ₂ O ₅	0.63	0.70	1.51	1.61	0.23
S	0.61				
Total	100.47*	99.93	99.86	99.92	(98.31)
S.G.	3.40	2.0	3.1	5.03	4.62
Normative minerals			Cation proportions	Basis 32(0)	Basis 6(0)
Qtz.	2.22	20.55	Si	0.104	
Or.	1.67	1.11	Al	0.898	
Ab.	13.64	1.57	Ti	1.636	1.869
An.	24.79		Fe ³⁺	13.090	0.245
Cor.	2.80	18.25	V	0.313	0.009
Hyp.	12.60	1.20	Mg	0.192	0.113
Mag.	28.51	23.37	Fe ²⁺	6.600	1.735
Haem.		12.28	Mn	0.017	0.034
Ilm.	10.59	12.59	Ca	0.007	0.012
Pyr.	1.20				
Ap.	0.67				

* Includes: Cu=trace, Ni=trace.

X-ray powder diffraction data, determined using Co K α radiation in an 11.483 cm diameter camera, gave a cubic cell dimension of $a = 8.395$ Å for magnetite 11406.

Chemistry of the opaque oxides

Analyses of magnetite and ilmenite appear in Table 1, together with their cation proportions. The marked excess of ferric iron in the magnetite is thought to be due to a combination of late crystallisation-oxidation and weathering. The effect of oxidation of magnetite during weathering can be seen in the magnetite lenses and ferruginised gabbro near the surface, where the mineral has been partially or completely replaced by haematite. Ilmenite, however, appears to be relatively unaltered, and the ferric iron occurs either as exsolved haematite or remains in solid solution.

Vanadium is concentrated in the magnetite relative to the coexisting ilmenite and has a similar distribution to that observed by Vincent and Phillips (1954) in the coexisting opaque oxides from the Skaergaard intrusion.

Manganese, on the other hand, is preferentially accommodated in the ilmenite lattice, as observed by Howie (1955) elsewhere. Buddington and Lindsley (1964) report an enrichment of Mn in coexisting ilmenite-magnetite from gabbroic rocks where Mn (magnetite)/Mn (ilmenite) = 0.65. The comparable distribution value for the Coates magnetite-ilmenite pair is 0.12. This ratio is identical with that found in Howie's Madras Series and also by the author

in the granulites from central Australia. The difference between these two values seems too large to be due to temperature alone, and may reflect more complete exsolution of the ilmenite phase from magnetite in both the Coates gabbro and the metamorphic rocks.

Petrogenesis of the magnetite gabbro

The Coates gabbro is thought to have been intruded as a partially crystallised residuum from a deep-seated gabbroic parent magma. Plagioclase tablets show an alignment parallel to the intrusive margins, consistent with them having been crystallised prior to emplacement. The opaque oxides, however, are interstitial and have crystallised after intrusion. Segregation of ilmenite granules within the magnetite precedes exsolution of haematite from ilmenite and ilmenite from magnetite. A temperature of formation of approximately 700° C, calculated from the analyses of magnetite and ilmenite according to the method of Buddington and Lindsley (1964), appears too low for a basic magmatic rock and may reflect removal of some coarse exsolved ilmenite from the magnetite during separation for analysis. The magnetite cell dimension indicates that almost all titanium has been exsolved and thus could be depleted during separation.

The small, solid magnetite lenses are explained as concentrations of interstitial liquids into tensional zones before complete solidification. Although the occurrence of these pods is restricted at Coates, it is conceivable that larger

scale "filter-pressing" of the residual magnetite-rich liquid could give rise to magnetite bodies similar to those occurring in Western Australia at Roebourne and Gabanintha (Simpson 1952 p. 124).

Cummingtonite occurs as colourless grains altering to sodic hornblende, but is not considered to be the primary ferromagnesian mineral. A reaction from earlier formed hypersthene or olivine, as suggested by Stewart (1946), appears more likely. No evidence, other than pronounced exsolution of iron ore droplets (as observed by Stewart in similar cummingtonite), was found for this mechanism.

Final enrichment of the residual liquid in sodium has caused replacement of cummingtonite and reaction at plagioclase-magnetite interfaces to give Na-hornblende.

Lateritisation

Lateritic rocks of three types occur in the vicinity of the Coates magnetite gabbro: pisolitic laterites and lateritic soils, residual laterites (derived by *in situ* ferruginisation and kaolinisation of the magnetite gabbro) and chemically transported laterites. Of these only the residual and transported laterites can be directly associated with the gabbro and will be considered further.

Residual laterites

The magnetite gabbro has suffered extensive weathering to a depth of 80-90 feet which has destroyed all the primary minerals (except the opaque oxides) and yet left the original texture intact. Two distinct zones of weathering may be recognised. A surface zone of concentration, varying between 10 and 20 feet in thickness, in which deposition of ferric iron has produced a hard ferruginous crust, still containing primary ore minerals and relict texture. Magnetite in this zone shows extensive alteration to haematite.

Below the ferruginous crust, friable kaolinised gabbro extends downwards to the fresh rock. Rocks in this zone are pink, white, buff or grey in colour and commonly show mottling. Original plagioclase crystals are replaced by pink and white kaolin boxworks, but magnetite and ilmenite seem relatively stable in the weathering environment. Leaching of material has occurred mainly from this zone and is indicated by the extremely low density of the rock. Depletion of Ca, Mg, Na, K and to a lesser extent Si during the weathering is most marked. A comparison between the normative minerals from the unaltered gabbro and the kaolinised gabbro gives an indication of the "minerals" that have been destroyed during the weathering and leaching processes (Table 1). The stability of ilmenite and the gradual oxidation of magnetite to haematite can also be seen. No sulphide minerals remain in the zone of weathering and oxidation. An attempt by Muskett *et al.* (1965) to establish a process to "up-grade" these laterites proved only partially successful.

Transported laterites

Limited exposures of dark chocolate-brown to purple-brown laterites occur on the western flank of the gabbro. These rocks have

a porous structure with cavities 2 to 10 mm in diameter. A vitreous to submetallic rim of oxides commonly surrounds these holes. The thickness of these laterites is not known, but they are at least 10 feet and probably not more than 25 feet thick.

The composition is unusual, with extremely high TiO_2 , Fe_2O_3 , Al_2O_3 and an enrichment of V_2O_5 relative to the magnetite gabbro (Table 1). The cations of these oxides would be precipitated from an alkaline aqueous solution, while Na^+ , K^+ , Ca^{++} , Mg^{++} , and to a lesser extent Mn^{++} , would remain in solution. Both the physical properties and composition of the laterites indicate that some chemical transfer and selective precipitation has been operative, and their formation has probably been controlled by an old water table (Fig. 4).

Conclusions

The Coates vanadium-bearing gabbro occurs as a sheet-like igneous intrusion. Strong flow-layering indicates that plagioclase was largely crystallised before intrusion, whereas interstitial crystallisation of magnetite and ilmenite occurred *in situ*. Late magmatic alteration of magnetite and cummingtonite has formed Na-hornblende.

The lenticular vanadium-bearing titaniferous magnetite bodies extending from Gabanintha to Barrambie, and also outcropping near Roebourne are thought to represent a similar igneous differentiation, from a gabbroic parent magma, to that suggested for the Coates gabbro, with the exception that only the non-crystalline (plagioclase deficient) portion has been mobilised and intruded.

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9.—South-western Australian occurrences of *Sthenurus* (Marsupialia, Macropodidae), including *Sthenurus brownei* sp. nov.

by D. Merrilees*

Manuscript received 21 February 1967; accepted 18 April 1967

Abstract

Specimens of *Sthenurus* from Mammoth Cave in the south-west of Western Australia have been re-examined and shown to fall into two groups, one with lower permanent premolars exceeding 16 mm in length, the other with lower permanent premolars less than 16 mm in length. These two groups are interpreted as distinct species rather than as sexual morphs. One of the species is *Sthenurus occidentalis* Glauert 1910, and a revised concept of this species is presented. The other species is newly described under the name *Sthenurus brownei*. The horizontal ramus of the mandible in *S. brownei* is much deeper behind M_4 than below the P_4-M_1 interspace, in contrast with any other described species of *Sthenurus* in which mandibular form is known.

Both *S. occidentalis* and *S. brownei* are shown to occur in Strong's Cave, near Mammoth Cave, and *S. brownei* is shown to occur also at Wanneroo, near Perth.

Introduction

While examining specimens of *Sthenurus* from Mammoth Cave, Western Australia, I became aware that two forms could be distinguished on the morphology and size of the lower permanent premolars and the lower incisors. Size and morphology of other teeth in these two forms were very similar. I have examined two alternative reasons for the observed incisor and premolar differences, namely sexual dimorphism and specific difference. Marked differences in many non-dental characters, and less marked differences in upper incisors, upper permanent premolars, upper molars and lower molars lead me to conclude that two different species of *Sthenurus* are represented in the Mammoth Cave sample.

Up to this time, the Mammoth Cave sample of *Sthenurus* has been assumed to represent only one species (*S. occidentalis* Glauert 1910), and other species of *Sthenurus* have been defined partly by comparison with this supposedly homogeneous sample from Mammoth Cave, as for example *S. oreas* by Bartholomai (1963) and *S. oreas* and *S. orientalis* by Tedford (1966). I have therefore thought it desirable to describe the differences between the two Mammoth Cave species in some detail.

Both species represented in the Mammoth Cave sample appear also to be represented in deposits in Strong's Cave (about 7 miles S. of Mammoth Cave), while the species newly described from Mammoth Cave appears also to be present at Wanneroo, in the Perth metropolitan region.

A *Sthenurus* premolar, probably representing *S. gilli* Merrilees 1965, is known from Madura Cave on the Nullarbor Plain (Lundelius 1963), and this occurrence has been discussed previously (Merrilees 1965). *Sthenurus* is also reported from the Balladonia district, on the western margin of the Nullarbor Plain (Glauert 1912). Neither of these occurrences is further considered in the present paper, which is confined to occurrences of *Sthenurus* in the South West Division as delimited by the 1966 edition of the Geological Map of Western Australia issued by the Geological Survey of Western Australia (Mines Department, Perth).

Copies of raw data on tooth dimensions in the south-western Australian samples of *Sthenurus* described herein have been lodged in the libraries of the Western Australian Museum (Beaufort St., Perth), the National Museum of Victoria (Russell St., Melbourne C1) and the Queensland Museum (Gregory Terrace, Brisbane). For statistical purposes, each individual animal has been represented only once for each dimension (see note, Merrilees 1965 p.24); all teeth were measured at the crowns, and all measurements were maximal, save that "width" in molars was measured across the proto-loph (id). "Depth" in lower incisors represents a measurement perpendicular to the long axis of the tooth. Data have been tabulated in the same form as used in previous discussions of relatively large samples of *Sthenurus* by Marcus (1962) and Merrilees (1965).

There is an unfortunate confusion in premolar tooth nomenclature in the macropodids, introduced by Stirton (1955) and followed by several other writers, e.g. Marcus (1962); Lundelius (1963); Bartholomai (1963); Tedford (1966). Tedford (1966) in his review of *Sthenurus* sets out his reasons for adopting this new nomenclature to replace the older nomenclature, established by

* Western Australian Museum, Perth, Western Australia.

Oldfield Thomas (1887) and adopted by nearly all later writers on marsupials. It appears that both systems are based prematurely on matters of tooth homology at present little understood either from embryological or from palaeontological studies. To facilitate comparison of reports using opposing systems of premolar designation, I have used vernacular names wherever convenient. Thus I refer below to the "deciduous premolars" ($P^{3/3}$ on the Thomas nomenclature, $P^{2/2}$ on the Stirton nomenclature) the "milk molars" (Thomas' $DP^{4/4}$, Stirton's $DP^{3/3}$) and the "permanent premolars" (Thomas' $P^{4/4}$, Stirton's $P^{3/3}$). However, where these circumlocutions are not convenient, I have retained the older Thomas nomenclature (see Thomas 1922, Ride 1964).

By courtesy of the curators of the fossil collections in other Australian museums, I have been able to make direct comparisons between the Mammoth Cave specimens and specimens of *S. atlas* from Wellington Caves (Aust. Mus. Syd. F 29556, 29558, 29575, 29582, 29584, 29585, 47052, 47059, 47063 and W. Aust. Mus. 66.10.11, cast of holotype), *S. andersoni* from King's Creek, Darling Downs (Qd. Mus. F 3813), *S. antiquus* from the Darling Downs (Qd. Mus. F 2931 and 2932), *S. oreas* from Gore, Queensland (Qd. Mus. F 3814), and *S. gilli* from Strathdownie, Victoria and from Naracoorte, South Australia (the numerous Nat. Mus. Vict. and S. Aust. Mus. specimens listed by Merrilees 1965), as well as numerous specimens of less certain identity from other localities in N.S.W., Victoria, King Island, and South Australia. For other comparisons, I have relied upon the published descriptions, dimensions and illustrations cited below, and have allowed for large discrepancies between the measurements recorded under the same names (e.g. "lengths" of molars) by different observers, because there are no standardized methods of measuring marsupial teeth (cf. Tedford 1966).

The Mammoth Cave deposit

Mammoth Cave is in an outcrop of calcareous aeolianite in the south-western portion of Western Australia, between Capes Naturaliste and Leeuwin. Numerous remains of marsupials and other vertebrates have been collected from this cave, mainly by L. Glauert in the early years of the present century. The fossiliferous deposit appears to have been part of a talus fallen through holes in the roof of the cave; it is certainly older than 31,000 radiocarbon years B.P. (Tamers, Pearson & Davis 1964) and probably older than 37,000 years B.P. (Lundelius 1960), according to estimates of the age of charcoal samples collected recently from what little remains of the deposit. I have shown (Merrilees, Ph.D. dissertation) that the age of the aeolianite in which the cave is cut cannot exceed late Milazzian (Oakley 1964), that probably the age of the deposit in the cave does not exceed the early phases of the Last (Würm or Wisconsin) Glaciation, and that the whole fossiliferous deposit probably accumulated in a relatively short time.

* Named after I. A. and W. R. Browne, whose research and teaching respectively in palaeontology and Pleistocene events (among their other geological interests) have provided stimulus to many students including myself.

The holotype of *Sthenurus occidentalis* was among the first (and hence presumably youngest) specimens collected from the Mammoth Cave deposit (Glauert 1910b). As holotype for the second *Sthenurus* species about to be described, I have selected a specimen which probably also came from the upper part of the deposit; the two holotypes must be of very nearly the same age.

The *Sthenurus* sample from Mammoth Cave

This consists of a great deal of material not bearing teeth, little of which has been studied or even catalogued, and 167 catalogued tooth-bearing specimens upon which the present paper is largely based. In addition Tedford (1966) reports the presence of 12 *Sthenurus* specimens from Mammoth Cave now in the Museum of Palaeontology, University of California, which I have not examined; there is at least 1 specimen in the Chicago Natural History Museum, of which I have a plaster cast (W. Aust. Mus. 63.5.15) kindly supplied by W. D. Turnbull, and 1 or more specimens in the American Museum of Natural History and in the British Museum (Natural History). Criteria by which specimens may be referred to the genus *Sthenurus* are set out by Tedford (1966).

Of the 167 tooth-bearing specimens from Mammoth Cave available to me, 5 are not specifically identifiable, 53 are referred to *Sthenurus brownei* sp. nov. and 111 are referred to *S. occidentalis* on grounds detailed below. All specifically determinable tooth-bearing specimens are listed with the raw data mentioned above.

At least 13 individuals of *S. brownei* and at least 16 individuals of *S. occidentalis* contributed to the Mammoth Cave sample available to me. Despite these substantial numbers of individuals, *Sthenurus* (even counting both species together) is not the most abundant macropodid in the Mammoth Cave deposit as stated by Tedford (1966 p.6); in numbers of individuals or of specimens, it is far exceeded by *Setonix* (more than 140 individuals).

*Sthenurus brownei** sp. nov.

Sthenurus occidentalis (partim) Glauert, 1910, *Rec. West. Aust. Mus.* 1 : 31-36.

Holotype.—Western Australian Museum fossil vertebrate specimen 63.2.94, right mandibular ramus lacking upper portion of coronoid process, showing full adult dentition (i.e. I_1 , P_4 , M_{1-4}), ankylosed with small portion of left ramus showing damaged root of I_1 in alveolus. See Figures 1 and 2.

Type locality.—Mammoth Cave, Western Australia, $34^{\circ} 1\frac{1}{2}'$ S, $115^{\circ} 1\frac{1}{2}'$ E—Glauert excavation, north-central in cave.

Paratypes, same locality as holotype.—Portions of mandibles, W. Aust. Mus. specimens 63.2.39, 63.2.40 (+ 63.2.51), 63.2.41 (+ 63.2.48), 63.2.42 (+ 63.2.50), 63.2.43 (+ 63.2.46), 63.2.44, 63.2.81 (+ 63.2.49), 63.2.82, 63.2.89 (+ 63.2.95), 65.3.16, 66.9.43.

Other specimens referred to *S. brownei*, same locality as holotype.—

(a) Mandibular specimens 63.2.55, 63.2.63-64, 63.2.84, 63.2.105, 63.2.197, 65.3.15, 65.4.38, 65.12.5. Geological Survey of Western Australia specimen no. 10087—see Note by Glauert 1910b, p. 62.



Fig. 1.—Holotype, *Sthenurus brownei*, Mammoth Cave, Western Australia. Buccal view. Note tapering of ramus towards front, high masseteric crest, short masseteric fossa.

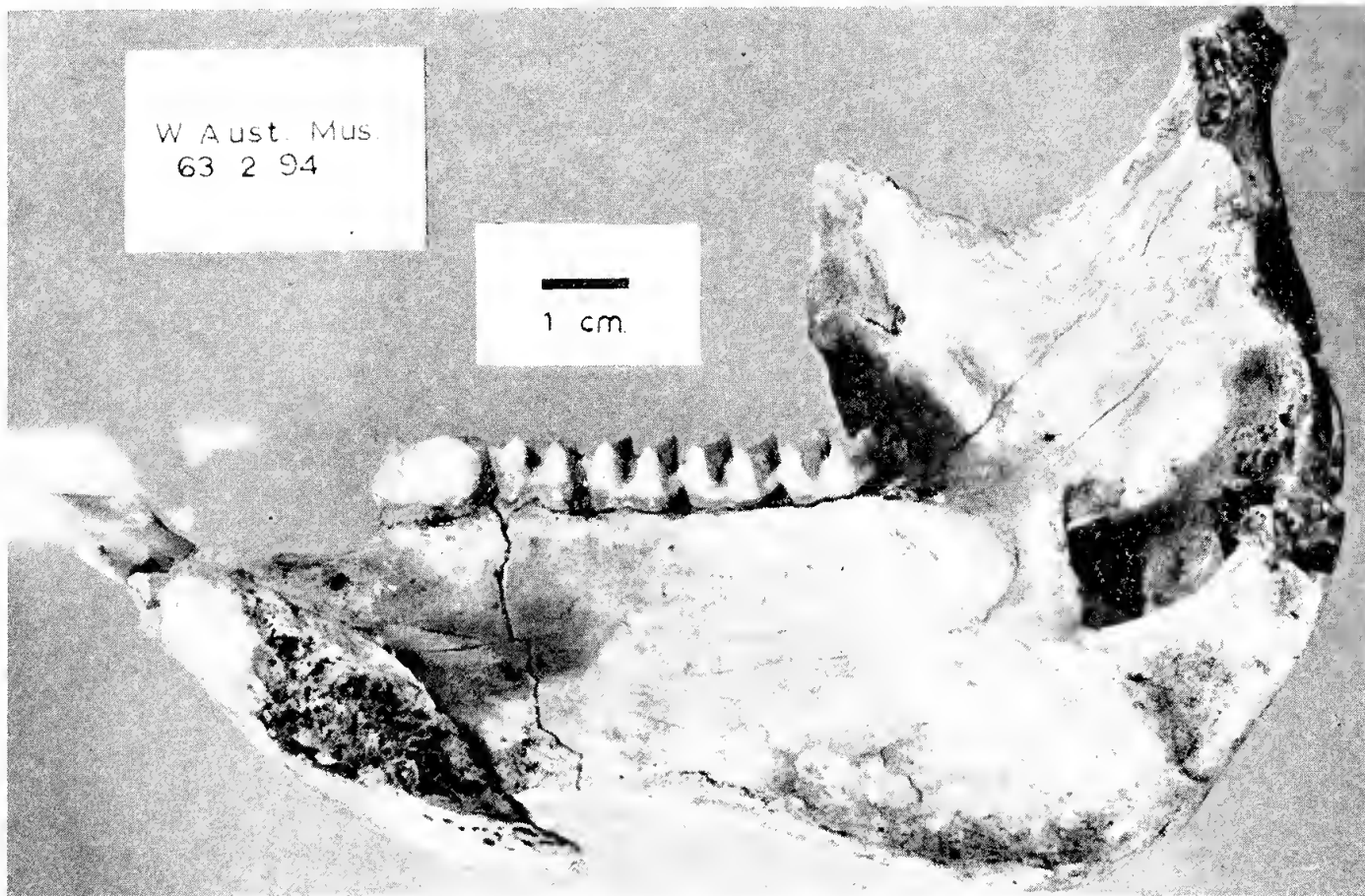


Fig. 2.—Holotype, *Sthenurus brownei*, Mammoth Cave, Western Australia. Lingual view. Note that crest bounding pterygoid fossa terminates in small sharp process.

(b) Maxillary and premaxillary specimens 63.2.116, 63.2.120, 63.2.124, 63.2.133, 63.2.135 (+ 63.2.141), 63.2.140, 63.2.145 (+ 63.2.144 + 63.2.148), 63.2.165, 63.2.167, 63.2.171, 63.2.174, 63.2.176, 63.2.179 (+ 63.2.143), 63.2.182, 63.2.185, 63.2.198, 63.5.8, 64.12.13, 65.4.36, 66.9.44-45. Cast 63.5.15.

(In the foregoing lists of specimens, numbers added in brackets refer to specimens catalogued separately but subsequently judged to derive from the same individual animal.)

Diagnosis.—Lower permanent premolar shorter than in *S. occidentalis*, but longer than longest (i.e. third) lower molar, and conspicuously longer than first lower molar. Lower incisor smaller than *S. occidentalis*, about same size as *S. gilli*.

Lower molars with well-marked posterior cingulum; about as wide at crest of proto-lophid as near base of enamel. Postero-buccal crest on lower permanent premolar extends further forward than mid-point of tooth before curving inward towards lingual crest.

Horizontal ramus of mandible much deeper behind M_4 than below P_4 - M_1 interspace, giving mandible the appearance of tapering towards front; lowest part of masseteric crest nearly as high as alveoli of molars, and thin; masseteric fossa (level with top of mandibular foramen) conspicuously shorter antero-posteriorly than *S. occidentalis*; crest bounding pterygoid fossa terminates anteriorly in small sharp process. *Comparison of S. brownei with other species, and description.*—

TABLE 1

Tooth dimensions in Sthenurus brownei from Mammoth Cave, Western Australia—holotype, paratypes, referred specimens.

Upper							
Dimensions Examined	Number of specimens		Observed Range mm	Sample Mean mm	Sample Standard Deviation mm	Sample Coefficient of Variation	
	Left	Right					
Length deciduous premolar P ³	5	9.8—11.0	10.46	0.47	4.5	
Width deciduous premolar P ³	4	9.4—9.8	9.53	0.16	1.7	
Length milk molar DP ⁴	5	9.5—10.5	10.00	0.37	3.7	
Width milk molar DP ⁴	4	9.4—10.5	9.88	0.47	4.8	
Length permanent premolar P ⁴	2	14.1—16.8	15.93	0.99	6.2	
Width permanent premolar P ⁴	2	11.0—13.1	12.00	0.72	6.0	
Length first molar M ¹	6	10.2—11.4	10.80	0.46	4.2	
Width first molar M ¹	6	10.4—11.7	10.93	0.48	4.4	
Length second molar M ²	7	10.6—12.0	11.40	0.48	4.2	
Width second molar M ²	6	11.1—12.0	11.47	0.36	3.1	
Length third molar M ³	6	11.5—12.1	11.80	0.27	9.9	
Width third molar M ³	6	11.1—11.8	11.48	0.25	2.2	
Length fourth molar M ⁴	3	10.9—11.5	11.27	0.32	3.2	
Width fourth molar M ⁴	3	10.6—11.5	11.04	0.45	4.1	
Lower							
Dimension Examined	Holotype W. Aust. Mus. 63.2.94	Number of specimens (including holotype where relevant)		Observed Range mm	Sample Mean mm	Sample Standard Deviation mm	Sample Coefficient of Variation
		Left	Right				
Depth incisor I ₁	9.5		4	9.2—10.6	9.78	0.60	5.4
Length deciduous premolar P ₃			5	8.7—9.2	8.92	0.19	2.1
Width deciduous premolar P ₃			5	7.3—8.1	7.78	0.33	4.2
Length milk molar DP ₄			5	8.5—9.6	9.20	0.46	5.0
Width milk molar DP ₄				8.4—8.8	8.52	0.09	1.1
Length permanent premolar P ₄	14.7	3	7	13.2—15.3	14.42	0.60	4.2
Width permanent premolar P ₄	9.9	3	8	9.0—10.0	9.64	0.38	3.9
Length first molar M ₁	10.8	11		9.3—11.0	10.21	0.40	3.9
Width first molar M ₁	9.2	10		8.6—9.5	9.08	0.29	3.2
Length second molar M ₂	11.5		9	10.5—11.5	11.09	0.36	3.2
Width second molar M ₂	9.9		8	9.3—10.3	9.94	0.37	3.7
Length third molar M ₃	12.0		7	11.1—12.1	11.57	0.39	3.4
Width third molar M ₃	10.3		7	9.7—10.7	10.21	0.24	2.4
Length fourth molar M ₄	11.2	4		11.1—11.5	11.33	0.15	1.3
Width fourth molar M ₄	10.4		4	10.2—10.5	10.33	0.15	1.5

TABLE 2

Tooth dimensions in *Sthenurus occidentalis* from Mammoth Cave, Western Australia—as revised.

Upper

Dimension Examined	Number of specimens		Observed Range mm	Sample Mean mm	Sample Standard Deviation mm	Sample Coefficient of Variation
	Left	Right				
Length deciduous premolar P ³	4		10.5—10.8	10.68	0.15	1.4
Width deciduous premolar P ³	4		9.0—9.7	9.42	0.30	3.2
Length milk molar DP ⁴	4		9.0—10.1	9.60	0.55	5.7
Width milk molar DP ⁴	4		10.2—11.3	10.63	0.50	4.7
Length permanent premolar P ⁴	5	7	16.9—18.8	17.58	0.61	3.5
Width permanent premolar P ¹	6	7	11.8—13.9	12.73	0.58	4.6
Length first molar M ¹		14	10.6—11.4	10.94	0.24	2.2
Width first molar M ¹		15	10.6—11.5	11.11	0.98	8.8
Length second molar M ²		16	11.2—12.0	11.55	0.25	2.2
Width second molar M ²		14	11.4—12.3	11.86	0.28	2.3
Length third molar M ³		14	11.6—12.4	12.05	0.22	1.8
Width third molar M ³		16	11.5—12.7	12.13	0.35	2.9
Length fourth molar M ⁴		8	11.1—11.5	11.36	0.17	1.5
Width fourth molar M ⁴		7	11.3—11.9	11.69	0.22	1.9

Lower

Dimension Examined	Holotype W. Aust. Mus. 60.10.2	Number of specimens (including holotype where relevant)		Observed Range mm	Sample Mean mm	Sample Standard Deviation mm	Sample Coefficient of Variation
		Left	Right				
Depth incisor I ₁	13.3	9		11.8—13.3	12.41	0.46	3.7
Length deciduous premolar P ₃		2		9.3—9.8	9.55	0.35	3.7
Width deciduous premolar P ₃		2		7.6—8.4	8.00	0.57	7.1
Length milk molar DP ₁		2		9.4—9.6	9.50	0.14	1.5
Width milk molar DP ₄		2		8.0—9.4	8.70	1.04	11.9
Length permanent premolar P ₄	16.8	12		16.3—17.6	16.74	0.36	2.2
Width permanent premolar P ₁	9.7	12		9.7—10.7	10.14	0.36	3.6
Length first molar M ₁	9.9		12	9.9—11.0	10.54	0.30	2.8
Width first molar M ₁	8.8		13	8.8—10.1	9.45	0.39	4.1
Length second molar M ₂	10.9	13		10.3—11.7	11.12	0.37	3.3
Width second molar M ₂	9.4	11		9.4—11.3	10.34	0.57	5.5
Length third molar M ₃	11.4		13	11.3—12.6	11.82	0.33	2.8
Width third molar M ₃	10.1		13	10.1—11.6	10.88	0.31	2.8
Length fourth molar M ₄	10.4	12		10.3—11.4	10.79	0.35	3.2
Width fourth molar M ₁	10.2	11		10.2—11.3	10.56	0.36	3.4

Species with which *S. brownei* must be compared:—

- S. atlas* Owen 1838
- S. andersoni* Marcus 1962
- S. notabilis* Bartholomai 1963
- S. tindalei* Tedford 1966
- S. occidentalis* Glauert 1910
- S. oreas* De Vis 1895
- S. pales* De Vis 1895
- S. antiquus* Bartholomai 1963
- S. orientalis* Tedford 1966
- S. gilli* Merrillees 1965

See illustrations of *S. brownei*—Figures 1-3 (holotype and a paratype showing adult lower dentition and other diagnostic characters of the mandible), Figures 4, 5, 6 (showing probable upper dentition and skull characteristics) and Table 1 (summary of tooth dimensions in holotype, paratypes and referred specimens from the type locality). See also Figure 8.

S. brownei distinguishable from all species named above, with the possible exception of *S. antiquus*, by tapering of horizontal ramus of mandible towards front (see Diagnosis above).

Further distinguishable from *S. notabilis* and *S. orientalis*, and probably from *S. tindalei*, *S. antiquus* and *S. pales* (in which the holotypes are skull fragments) by smaller size, and from *S. andersoni* and *S. gilli* by larger size, of lower molars. Upper molars smaller in *S. brownei* than in *S. tindalei* and *S. antiquus*, and probably in *S. pales* (and *S. orientalis* and *S. notabilis*?), and larger than in *S. andersoni* and *S. gilli*.

Differs from *S. atlas* in that width of lower permanent premolar exceeds crown height, and lower molars show abundant fine crenulations. Differs from *S. oreas* in that lower permanent premolar longer than any molar (upper or lower), and much longer (averaging about 40%

longer) than first lower molar. Differs from *S. occidentalis* in that lower incisor much smaller and lower permanent premolar shorter (less than 16 mm.); upper permanent premolar probably also shorter, but upper and lower molars similar in size, to *S. occidentalis*.

Upper molars here attributed to *S. brownei* (see below) show anterior shelf divided by ridge into smaller, smoother lingual portion and

larger buccal portion with abundant fine crenulations, and median valley enclosed buccally by longitudinal low crest. Upper permanent premolars here attributed to *S. brownei* show marked vertical ridges on buccal faces, and most anterior lingual cusp nearly as prominent as most anterior buccal cusp.

For other mandibular and probable skull characteristics of *S. brownei*, see examples described in Tables 3 and 4 below.

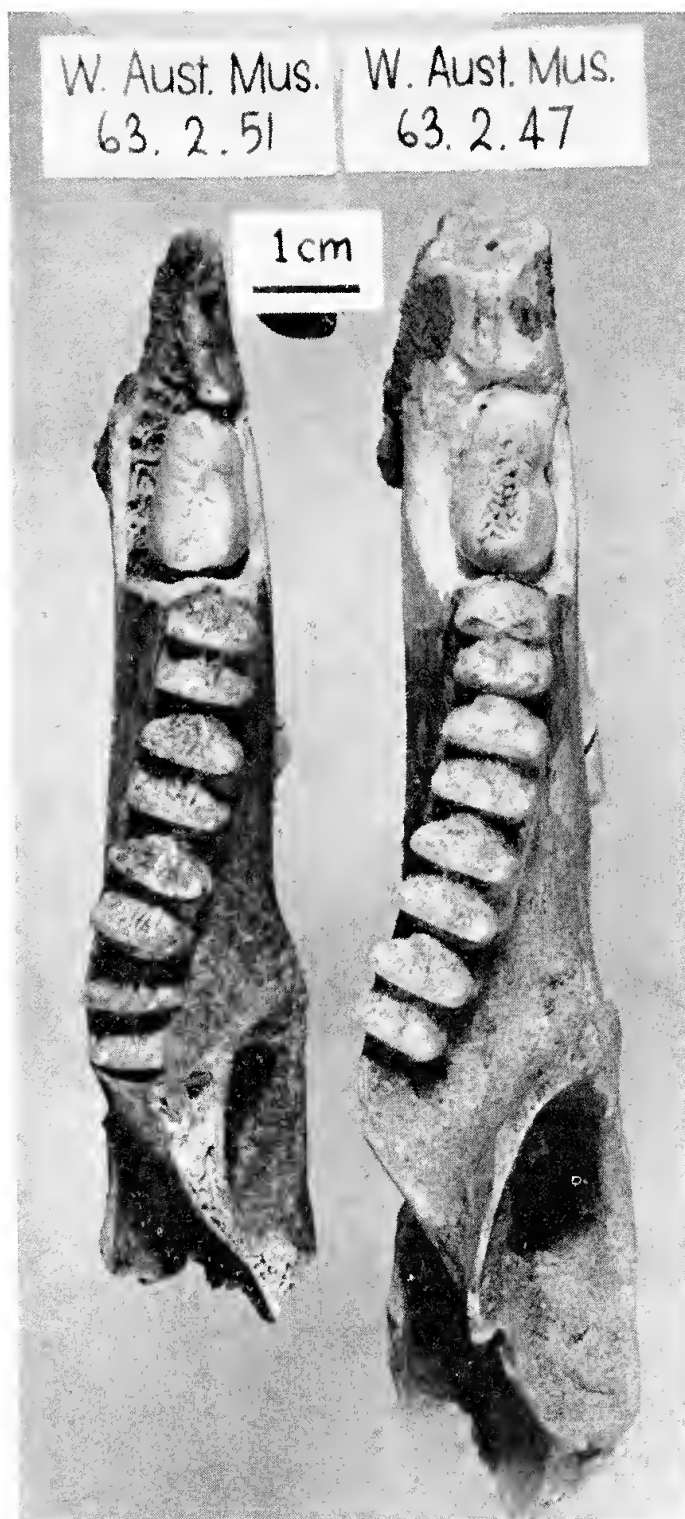


Fig. 3.—Comparison of mandibular cheek teeth in *S. brownei* (63.2.51) and *S. occidentalis* (63.2.47) from Mammoth Cave, Western Australia. Both specimens juveniles from which deciduous premolars and milk molars have been removed, exposing unerupted permanent premolar. Note difference in morphology and length in permanent premolars, more pronounced fine crenulation on molars in *S. brownei*.

Sthenurus occidentalis Glauert 1910

Sthenurus occidentalis (partim) Glauert, 1910 (before Feb. 2nd) *Rec. West. Aust. Mus.* 1: 31-36, pl. 5, figs. 6-7.

Holotype.—Western Australian Museum fossil vertebrate specimen 60.10.2, major portion of mandible lacking upper parts of coronoid and condylar regions, full adult dentition on both sides.

Described by Glauert (1910a) with photographs of right buccal and occlusal aspects ("Plate V, figs. 6 and 7", printed as separate plates). Collected by E. A. Le Souef in 1904 in two portions, later fitted together by L. Glauert ("The West Australian" Feb. 2nd, 1910, p. 4), the larger portion described by Glauert (1910b) with photographs of occlusal, left buccal and left lingual aspects (Plates 10-12).

Type locality.—Mammoth Cave, Western Australia, 34° 1½' S, 115° 1½' E—probably on margin of Glauert excavation, north-central in cave (Merrilees, Ph.D. dissertation).

Paratypes.—Descriptions of specimens by Glauert (1910a) and his internal Museum records do not permit certain recognition of all his paratypes nor of their precise location in Mammoth Cave. However, their location probably is near that of the holotype (Merrilees Ph.D. dissertation). Specimens 63.2.74 probably and 63.2.194 certainly are paratypes and certainly fall within my revised concept of *S. occidentalis*. Specimens 63.2.195-196 are paratypes and probably fall within my revised concept of *S. occidentalis*. Specimen 63.2.197 and some other juvenile specimens not now recognizable are paratypes but are referred by me to *S. brownei* sp. nov. See Discussion below.

Other specimens from Mammoth Cave, referred by me to *S. occidentalis*.—

(a) Mandibular specimens 61.7.57 (+ 63.2.83), 63.2.45, 63.2.47 (+ 63.2.67), 63.2.52-54, 63.2.56-62, 63.2.65-66, 63.2.68-71, 63.2.73, 63.2.75 (+ 63.2.92), 63.2.76-80, 63.2.85, 63.2.87-88, 63.2.91, 63.2.96-101, 63.2.102 (+ 63.2.114), 63.2.103-104, 63.2.115, 63.2.118, 63.2.161.

(b) Maxillary and premaxillary specimens 62.4.3-6, 62.4.8, 62.8.31, 63.2.119, 63.2.123, 63.2.125-132, 63.2.134, 63.2.138 (+ 61.7.58 + 63.2.136), 63.2.139, 63.2.142 (+ 63.2.137), 63.2.147, 63.2.149, 63.2.151-156, 63.2.162-164, 63.2.166, 63.2.168, 63.2.169 (+ 62.4.7), 63.2.170, 63.2.172-173, 63.2.175, 63.2.177-178, 63.2.180-181, 63.2.183-184, 63.2.186-190, 66.7.10-11, 66.8.7, 66.9.51.

(In the foregoing lists of specimens, numbers added in brackets refer to specimens catalogued separately but subsequently judged to derive from the same individual animal.)

Revised diagnosis.—Lower permanent premolar longer than in *S. brownei*, conspicuously longer than any molar. Lower incisor larger than *S. brownei* or *S. gilli*.

TABLE 3

Comparison of Western Australian Museum specimen 63.2.94 (holotype of *S. brownei*) with 60.10.2 (holotype of *S. occidentalis*) from Mammoth Cave.
(Both specimens show adult mandibular dentition. Measurements in mm)

	63.2.94	60.10.2 (Right side)
Depth incisor	9.5 (may be reduced by wear).	13.1
Incisor incumbency: angle between long axis of incisor and occlusal plane of cheek teeth	30–35° (i.e. more procumbent).	40–45° (i.e. more incumbent).
Upper aspects of symphysis immediately behind incisors	shallow U-shape.	deep V-shape.
Upper aspects of symphysis immediately behind genial pits	broad, gently sloping shelf.	narrow, steeply sloping shelf.
Length x width permanent premolar; wear stage	14.7 x 9.9; I/II	16.8 x 9.7; II
Crown height permanent premolar (postero-lingual)	8.4	8.5
Form of permanent premolar; occlusal surface	long lingual crest; postero-buccal crest reaches further forward than half-way along tooth.	long lingual crest; postero-buccal crest reaches forward about half-way along tooth.
Form of permanent premolar; horizontal section near base of enamel	buccal embayment present but not marked; projection in front of anterior cusp small.	marked buccal embayment; extensive projection in front of anterior cusp.
Length x width first molar; wear stage	10.8 x 9.2; M	9.9 x 8.8; B
Length x width second molar; wear stage	11.5 x 9.9; E	11.1 x c. 9.7; B
Length x width third molar; wear stage	12.0 x 10.3; B	11.4 x 10.1; B
Length x width fourth molar; wear stage	11.2 x 10.4; B	10.2 x 10.0; B
M ₃ protolophid; width near occlusal surface	10.0	9.2
M ₃ protolophid; width near base of enamel	10.2	10.0
M ₃ hypolophid; width near occlusal surface	10.1	9.0
M ₃ hypolophid; width near base of enamel	10.2	9.9
Form of M ₁ ; transverse vertical section through hypolophid	sides converge downwards.	sides diverge downwards.
Form of molars; posterior cingulum	small but distinct shelf.	mere swelling near base of enamel.
Form of molars; minor ornamentation and links	present; fore-link and mid-link weak.	present; fore-link and mid-link very weak.
Vertical height of ramus below P ₄ —M ₁ interspace	33	34
Vertical height of ramus immediately behind M ₁	45	38 (L. side).
Position below which lower border of ramus descends lowest	posterior border of coronoid process.	immediately behind M ₁ .
Lowest point of masseteric crest	a little below level of molar alveoli.	below level of molar alveoli.
Lateral thickness of masseteric crest at lowest point	2	4½
Lateral thickness of anterior border of coronoid process at M ₄ occlusal level	3	5
Antero-posterior length of masseteric fossa level with top of mandibular foramen	22	35
Maximum lateral width of lower rear part of ramus surrounding mandibular foramen	23	28
Crest bounding pterygoid fossa	terminates anteriorly in small sharp process; deep sulcus between this process and small ridge diagonally placed on lingual face of horizontal ramus.	slight sulcus interrupts smooth confluence with lingual face of horizontal ramus.
Digastric sulcus, maximum forward extent	below anterior M ₁ .	below anterior M ₂ .
Posterior mental foramen	below anterior M ₂ .	below anterior M ₂ .

Lower molars show little or no posterior cingulum; wider at base of enamel than at transverse occlusal ridges. Lower permanent premolar with pronounced buccal embayment; postero-buccal crest curves inward towards lingual crest about half way along tooth.

Horizontal ramus of mandible about same depth behind M₄ as below P₄M₁ interspace, lowest part of masseteric crest falls far below level of molar alveoli, and thick; masseteric fossa (level with top of mandibular foramen)

longer antero-posteriorly than *S. brownei*; crest bounding pterygoid fossa nearly confluent with lingual wall of horizontal ramus.

Comparison of S. occidentalis with other species, and revised description.—

(Same comparisons required as with *S. brownei* above.)

See illustrations of holotype of *S. occidentalis* provided by Glauert 1910a, b. See also Figures 3, 4 below (direct comparisons of lower and

TABLE 4

Comparison of Western Australian Museum specimen 63.2.198 (skull of *Sthenurus browni*) with 62.8.31 (skull of *S. occidentalis*) from Mammoth Cave.

(The specimens represent juvenile animals, 63.2.198 being smaller than 62.8.31 and with M⁴ not fully erupted. Measurements in mm.)

	63.2.198	62.8.31
Maximum diameter of root of left I ¹ near enamel margin, perpendicular to long axis of tooth	7.0	10.0
Maximum diameter of root of left I ² near enamel margin, perpendicular to long axis of tooth	4.4	4.3 (right)
Maximum diameter of root of left I ³ near enamel margin, perpendicular to long axis of tooth	7.6	c. 7.6 (right)
Minimum distance between alveolar margins of I ² teeth of opposite sides	9.1	c. 10.3
I ³ , lingual surface of crown	smooth	(I ³ not present)
Distance between alveolar margins of I ³ teeth of opposite sides, about central, internal margins	12.7	13.0
Incisive foramina, posterior endings	narrow slits	rounded
Prenaxillary-maxillary sutures behind incisive foramina	project far backwards	end at foramina
Posterior palatal vacuities, anterior margins level with:—	posterior P ³	posterior DP ¹
Length x width, and wear, of P ³ : side measured	10.7 x 9.5, H1; R	10.8 x 9.6, H1; L
Length x width, and wear, of DP ¹ : side measured	10.1 x 10.5, M; R	9.8 x 10.2, M; L
Length x width, and wear, of P ² : side measured	16.2 x 12.4, L; R	c. 18 x 13.0, L; L
Form of P ³	many minor crenulations	few minor crenulations
Form of DP ¹	many minor crenulations	few minor crenulations
Form of P ¹ —most anterior lingual and buccal cusps	lingual nearly as prominent as buccal	buccal far more prominent than lingual
Form of P ¹ —buccal face	strongly ridged	weakly ridged
Length x width, and wear, of M ¹ : side measured	11.1 x 10.3, E; R	10.3 x 10.9, E; L
Length x width, and wear, of M ² : side measured	12.0 x 11.0, B; R	11.4 x 11.7, B; L
Length x width, and wear, of M ³ : side measured	12.1 x 11.2, B; R	11.7 x 12.3, B; L
Length x width, and wear, of M ⁴ : side measured	c. 11.1 x 10.6, U; R	11.1 x 11.6, B; L
Form of molars—general	minor crenulations very prominent, especially in central valley	minor crenulations present, but more subdued than 63.2.198
Form of molars—anterior shelf	divided into smaller, smooth lingual portion and larger, buccal portion with prominent minor ridglets	undivided: subdued ridglets throughout
Form of molars—central valley	enclosed buccally by longitudinal crest (also visible in DP ¹)	M ¹ partially closed buccally by low longitudinal crest, others open
Form of molars—posterior shelf, viewed in prone position	on buccal side, falls below anterior shelf of next succeeding molar	at no position lower than corresponding position on anterior shelf of next succeeding molar
Basisphenoid	long (c. 18)	short (c. 7)
Tympanic, ventral border	steeply sloping	almost horizontal
Tympanic—zygomatic cell	large	small
Condylar foramen, viewed in prone position	overhung by condyle	not overhung by condyle
Condyles, elongation, angle with vertical axis	c. 45°	c. 60°
Subsquamosal foramen	in shallow depression	in deep depression
Interparietal suture, rear portion	lies in deep depression between post-orbital crests	about same level as post-orbital crests
Fronto-parietal sutures	change direction abruptly from obliquely antero-posterior to lateral	curve smoothly round from obliquely antero-posterior to lateral
Orbit, minimum thickness at border of antero-ventral wall, level with infra-orbital foramen	2	6
Zygomatic process, anterior border descends opposite:—	posterior part of M ¹	anterior part of M ¹
Zygomatic process, anterior border near root	sharply ridged	rounded
Infra-orbital foramen	large, deeply recessed	small, opening from shallow cavity
Interpremaxillary suture, anterior portion	rises vertically above incisors, abruptly becoming horizontal	slopes upward and backward from incisors in smooth curve
Narial aperture, lower margin seen from in front	catenary curve	wide V shape
Maxillary-premaxillary suture, vertical ascent on external aspect of skull	opposite anterior ends of incisive foramina	opposite posterior ends of incisive foramina

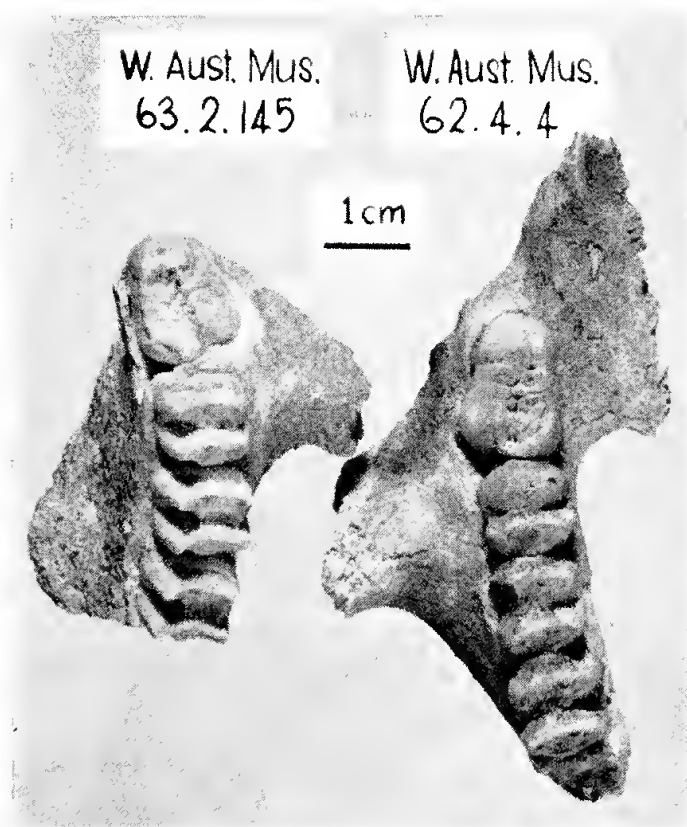


Fig. 4.—Comparison of maxillary teeth in *S. brownei* (63.2.145) and *S. occidentalis* (62.4.4) from Mammoth Cave, Western Australia. Note low bucal crest enclosing central valley of M^2 , 3 in 63.2.145.

probable upper cheek teeth in *S. occidentalis* and *S. brownei*), Fig. 7 (part of skull probably of *S. occidentalis*), and Table 2 (summary of tooth dimensions in holotype and specimens from same locality as holotype, referred by me to *S. occidentalis*).

Distinguishable from *S. notabilis* and *S. orientalis*, and probably from *S. tindalei*, *S. antiquus* and *S. pales* (in which the holotypes are skull fragments) by smaller size, and from *S. andersoni* and *S. gilli* by larger size, of lower molars. Upper molars smaller in *S. occidentalis* than in *S. tindalei*, *S. antiquus* and probably *S. pales* (also *S. orientalis* and *S. notabilis*?), and larger than in *S. andersoni* and *S. gilli*.

Differs from *S. atlas* in that width of lower permanent premolar exceeds crown height. Differs from *S. oreas* in that lower permanent premolar conspicuously longer than any molar (upper or lower), averaging 59% longer than first lower molar.

Differs from *S. brownei* in that lower incisor larger, lower permanent premolar longer (exceeds 16 mm.) and ramus about as deep below P_4 - M_1 interspace as immediately behind M_1 .

Differs from *S. orientalis* not only in having smaller (shorter and narrower) lower molars but in having lower permanent premolar longer relative to the lower molars. Lower permanent premolars of similar absolute lengths in *S. occidentalis* and *S. orientalis*.

Upper molars here attributed to *S. occidentalis* show anterior shelf more or less uniformly ornamented with subdued crenulations; crenu-



Fig. 5.—Skull of *Sthenurus brownei*, Mammoth Cave, Western Australia. Note thin crest forming antero-ventral border of orbit, and sharp ridge forming anterior border of zygomatic process.

lations present elsewhere on occlusal faces of upper molars, but less prominent than on *S. brownei*. Upper permanent premolars here attributed to *S. occidentalis* show weak vertical ridges on buccal faces, and marked inequality between most anterior buccal and lingual cusps (buccal much more prominent).

For other mandibular and probable skull characteristics of *S. occidentalis*, see examples described in Tables 3 and 4.

Despite the fact that Tedford (1966) was not aware of the existence of two *Sthenurus* species from Mammoth Cave, his diagnosis and description (p. 33 to end of second paragraph p. 36) and illustrations (Figs. 11, 12) of *S. occidentalis* require little amendment. Deletion of the comment "The median valley is closed labially in unworn teeth by a prominent thin crest from the paracone" (p. 34) and alteration of the comment on the masseteric crest (p. 33 and also p. 61) to read "masseteric crest descends below level of alveolar border" would make Tedford's description of *S. occidentalis* applicable to my revised concept of it.

Discussion

Specimen 63.2.94 is chosen as the holotype of *S. brownei* partly because the laminated structure of the material originally encrusting much of the specimen suggests that it may have come from stratigraphically higher parts of the deposit (as did the holotype of *S. occidentalis*), partly because the specimen could not have been used by Glauert (1910) to formulate his concept of "*S. occidentalis*" (since its teeth were then obscured by matrix except for part of the incisor) and partly because it represents the same part of an animal of about the same dental age as the holotype of *S. occidentalis*. The "diagnoses" and "comparisons with other species" above of *S. brownei* and *S. occidentalis* are based mainly on the respective holotypes.

There is thus little doubt that mandibular specimens bearing permanent premolars have been assigned correctly to one or the other Mammoth Cave species, and such specimens have been designated above as paratypes in the case of *S. brownei*. But there must be some doubt about mandibular specimens which do not show permanent premolars, and considerable doubt about the specific identity of any skull fragment, since there is no direct evidence associating any skull with any mandibular specimen. Mandibular specimens lacking the permanent premolar and all skull fragments have been considered, therefore, not to have the status of paratypes, but merely of specimens referred to their respective species with some measure of uncertainty, in spite of coming (with the possible exception of 10087—see note above) from the same circumscribed deposit as the holotypes and paratypes.

Table 3 above compares the holotypes of *S. brownei* and *S. occidentalis*, and Table 4 compares skull structures in the two most complete *Sthenurus* skulls recovered from Mammoth Cave. Table 4 records many differences between these skulls which cannot be attributed to differences of growth, since the animals concerned were of similar dental age. (Dental wear designations in Tables 3 and 4 are as used by Tedford 1966, pp. 4, 5.)

None of the numerous other *Sthenurus* skull fragments from Mammoth Cave shows all the diagnostic structures listed in Table 4, but there is little difficulty in assigning nearly all such specimens either to a group resembling skull 63.2.198 or to a group resembling skull 62.8.31, and these are the groups listed above under *S. brownei* and *S. occidentalis* respectively.

My reasons for assigning skull 63.2.198 and the fragments resembling it to *S. brownei* and skull 62.8.31 and the more numerous skull fragments resembling it to *S. occidentalis* are as follows. Skull 63.2.198 has a shorter permanent premolar with lingual and buccal crests of approximately equal height, and this is more consistent with the lower permanent premolars characteristic of *S. brownei* than with the longer, slightly more sectorial lower permanent premolars characteristic of *S. occidentalis*, in which the lingual crests greatly overshadow the buccal crests in P_4 teeth. The ratio of juveniles (with P^1 not yet erupted) to adults in the group resembling 63.2.198 is much higher than in the group resembling 62.8.31, and this too is more consistent with the mandibular specimens of *S. brownei* than *S. occidentalis*. There are at least 16 individuals represented in the 62.8.31 skull group, but it is possible to estimate the dental age in only 14 of these individuals; of these 14 only 5 are juveniles. At least 9 individuals are represented in the 63.2.198 skull group, and of these 9, 6 are juveniles. Among mandibular specimens, *S. occidentalis* is represented by at least 15 individuals of which 13 are of determinable dental age, only 2 of these being juveniles; whereas of at least 13 individuals of *S. brownei*, all of determinable dental age, 7 are juveniles. Skull 62.8.31 is of generally more robust construction than skull 63.2.198; for example, the antero-ventral borders of the orbits are thicker and more rounded in 62.8.31. Mandibles of *S. occidentalis* appear to be rather more robust than those of *S. brownei*; for example, the masseteric crest is thicker at its lowest point in *S. occidentalis* than in *S. brownei*. On grounds of greater robustness, it is perhaps reasonable to assign skull 62.8.31 to *S. occidentalis* and 63.2.198 to *S. brownei*.

Skull 63.2.198 (*S. brownei*) shows only right I^2 and I^3 and left I^2 of the incisor row, the other incisors being represented only by broken stumps in their sockets. Skull 62.8.31 (*S. occidentalis*) shows the broken stump of I^1 and I^2 of both sides, and empty alveoli of I^3 of both sides. Isolated upper incisors, and premaxillary specimens showing one or more incisors, are not readily separable into two clear-cut groups. Consequently upper incisors cannot be identified with confidence as *S. brownei* or *S. occidentalis*.

However, the I^3 remaining on 63.2.198 is of a strap-like form not unlike that illustrated for *S. gilli* by Merrilees (1965 Fig.6), and is smooth on the lingual face, while the I^2 teeth remaining on 63.2.198 are rather small by comparison with other I^2 teeth of *Sthenurus* from Mammoth Cave. It is reasonable to suggest that the upper incisor row in *S. brownei* should be smaller than that of *S. occidentalis* by analogy with the lower incisors, which are smaller in *S. brownei*. A complete set of upper incisors is preserved on specimen

63.2.144, which appears from the fit of broken edges to represent the front part of the same skull as maxillary specimen 63.2.145. Specimen 63.2.145 shows a short P^1 , and $M^1, 2, 3$ each with prominent minor ridglets, a divided anterior shelf, and a posterior shelf falling below the level of the anterior shelf of the next succeeding molar, and probably represents *S. brownei*. I assume that 63.2.144 also represents *S. brownei*, and this identification is also suggested by characters of the specimen itself such as vertical ascent of the premaxillary-maxillary suture opposite the forward part of the incisive foramen or abrupt change from vertical to horizontal in the profile below the narial aperture.

Specimen 63.2.144 may be contrasted with 63.2.152 in the ways discussed below, and I assume from these contrasts that 63.2.152 represents *S. occidentalis*. Other specimens bearing sthenurine upper incisors have been separated into two groups according to their resemblance to 63.2.144 or to 63.2.152.

The lingual face of I^3 in 63.2.144 differs from that of 63.2.152 both in profile and in the texture of the surface. I^3 in 63.2.144 is smooth on the lingual face, and the maximum width of the tooth is about half way down the crown; I^3 in 63.2.152 shows many minor crenulations, a pronounced fold in the enamel of the antero-lingual "corner", and a maximum width close to the occlusal edge. Viewed in the prone position, I^3 in 63.2.144 shows a slightly sigmoid section, with a slight lingual in-turning of the anterior border and a slight buccal out-turning of the posterior border. On the other hand, I^3

in 63.2.152 shows a more evenly curved section, with buccal convexity. In both specimens, both in prone and in buccal views, a thickening of I^3 along its antero-buccal border is evident. I^1 and I^2 are larger in 63.2.152 than in 63.2.144, but otherwise similar.

Early observations on the *Sthenurus* sample from Mammoth Cave

The holotype of *S. occidentalis* and at least one other *Sthenurus* specimen appear to have been collected by E. A. Le Souef very soon after fossil mammals were first discovered in Mammoth Cave in 1904. Le Souef identified his find as a new variety of *Sthenurus atlas*. He used the name *S. atlas hacketti* in a report made by him in 1904 or 1905 to the Caves Board, but this name appears not to have been published until Feb. 5th 1910, when Le Souef quoted extracts from his report in a letter to the Editor of "The West Australian" (a daily newspaper). Le Souef's letter appears to have been prompted by an article in the same newspaper three days earlier (Feb. 2nd 1910), which article mentions "the first volume of the Records of the Museum and Art Gallery", carrying Glauert's description of *S. occidentalis*. I accept Glauert's publication of the name *S. occidentalis* as antedating Le Souef's *S. atlas hacketti* by a few days. Woodward (1909) mentions Glauert's intention to use the name *S. occidentalis*, probably for 60.10.2, but gives no description; Glauert (1909) mentions but does not name his new species. Glauert appears to have described the incomplete mandible (part of 60.10.2—see above) in

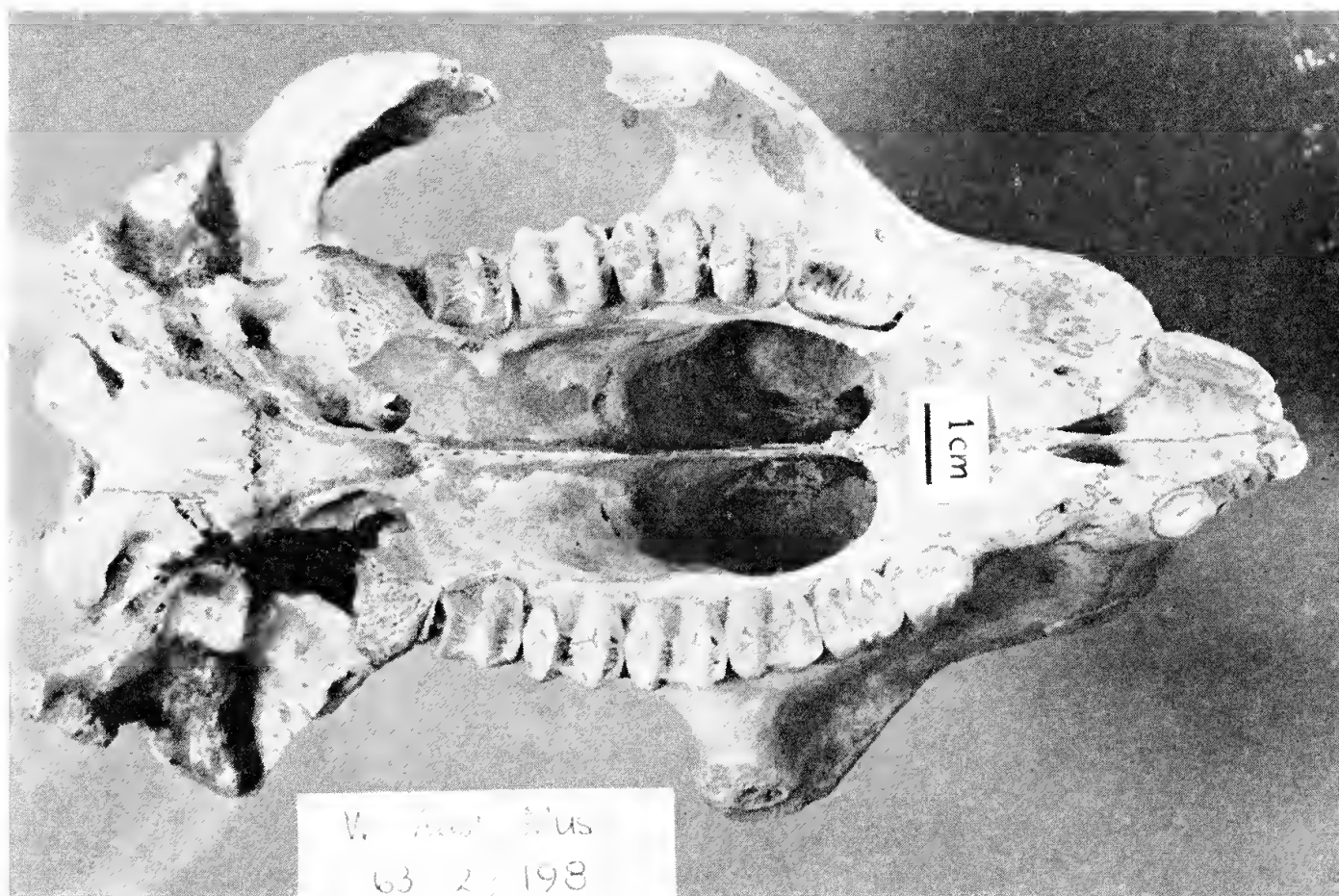


Fig. 6.—Skull of *Sthenurus brownei*, Mammoth Cave, Western Australia. Right permanent premolar exposed by removing deciduous premolar and milk molar. (Same specimen shown by Anderson 1932, Plate 45, Fig. 1.)

a report to the Caves Board, part of which report also was published in 1910, but not before March 21st, since that date appears on the Government Geologist's "Prefatory Note" to Bulletin 36, Geological Survey of Western Australia, which carried Glauert's description. Le Souef's report to the Caves Board, including the name *Sthenurus hacketti*, was quoted again in "The West Australian", Feb. 21st 1914; but *S. atlas hacketti* (or *S. hacketti*) appears not to have been used since then.

Glauert's description of *S. occidentalis* (1910a—Rec. West. Aust. Mus. 1) clearly designates the specimen now catalogued as 60.10.2 as the holotype, and mentions also some other specimens, not all of which can now be recognized with certainty. However, it is probable that some of these specimens (63.2.194-196, 63.2.74) are referable to *S. occidentalis* as revised by me, while some (63.2.197 and some juvenile specimens) are referable to *S. brownei*. In fact,

Glauert mentions characters that I consider diagnostic of *S. brownei*; referring probably to 63.2.197, Glauert states that "The ramus . . . is more slender and has a decided angle at the posterior lower end of the horizontal ramus in place of the graceful curve that characterises *S. occidentalis*." However, he adds that this is a "character which loses its sharpness as the animal increases in size", whereas the holotype of *S. brownei* comes from an adult animal but still shows this character quite clearly. Elsewhere, Glauert (1910b) draws attention to differences between the permanent premolar in specimen 10087 and the holotype of *S. occidentalis*, but dismisses these differences as individual variations.

Anderson (1932) reports his examination of two skulls from Mammoth Cave, his specimen A (now catalogued as 62.8.31, *S. occidentalis*) and specimen B (now catalogued as 63.2.198, *S. brownei*, figured by Anderson, Plate 45, Fig. 1). Anderson draws attention to differences between 62.8.31 and 63.2.198, but does not suggest that they represent distinct species.

Anderson (1932) also describes and figures a specimen from King Island, his specimen C, from the collection of the Queen Victoria Museum and Art Gallery, Launceston. I have been able to examine this specimen, and have concluded that it resembles 62.8.31 more closely than 63.2.198, although it is rather small. Glauert (1948) reproduces what appears to be a reversed print of Anderson's (1932) Plate 46, Figure 1 (showing the King Island specimen) as part of a discussion on fossils from Mammoth Cave; Glauert's (1948) plate, like Anderson's original, is labelled *S. occidentalis*.

Possibility of sexual dimorphism in the Mammoth Cave sample of *Sthenurus*

Sexual dimorphism in various skeletal elements, even in tooth dimensions, is well-known in mammals; for example Kurtén and Rausch (1959) demonstrate significant differences between the sexes in three tooth dimensions in the Alaskan wolverine (*Gulo gulo*) and Ride (1964) similarly in five tooth dimensions in the modern Tasmanian "wolf" or "tiger" (*Thylacinus cynocephalus*). I have examined various samples of modern macropods for sexual dimorphism in tooth dimensions, and have found some significant differences; also I have shown that data on the modern red kangaroo (*Megaleia rufa*—see Ride 1962) published by Sharman, Frith and Calaby (1964 Table 4) reveal significant differences between the sexes at least in respect of posterior width of P⁴, length of P⁴ and width of M¹. However, the magnitude of these differences between the sexes in modern samples in no case approaches the magnitude of the difference between lengths of the lower permanent premolars in the two groups discernible in the Mammoth Cave fossil sample of *Sthenurus*. See Table 5. Furthermore, I know of no example of sexual dimorphism in tooth form such as those clearly shown by lower permanent premolars in the two kinds of *Sthenurus* from Mammoth Cave, or somewhat less clearly by the upper permanent premolars or upper or lower molars. Nor am I aware of any example of sexual dimorphism in so many non-dental structures as those listed above for the Mammoth Cave *Sthenurus*.

TABLE 5

Relative magnitudes* of differences in tooth dimensions between sexes in some modern macropod samples and between two groups in the fossil *Sthenurus* sample from Mammoth Cave.

Sample	Tooth dimension examined	Difference between means within sample	Mean of females or <i>S. brownei</i>	Magnitude of difference
		mm	mm	%
<i>Protemnodon bicolor</i>	Length P ⁴	0.30	9.60	3.1
<i>Bettongia penicillata</i>	Width M ¹	0.21	4.03	5.2
<i>Protemnodon agilis</i>	Width M ¹	0.36	6.33	5.7
<i>Macropus robustus</i>	Width M ¹	0.50	7.28	6.9
<i>Macropus robustus</i>	Length P ⁴	0.70	7.67	9.1
† <i>Megaleia rufa</i>	Width M ¹	0.59	7.56	7.8
† <i>Megaleia rufa</i>	Length P ⁴	0.72	6.96	10.3
<i>Sthenurus</i> , Mammoth Cave	Length P ⁴	1.65	15.93	10.4
<i>Sthenurus</i> , Mammoth Cave	Length P ₄	2.32	14.42	16.1

* Relative magnitudes stated as percentages: difference in arithmetic mean for stated dimensions between groups within sample as proportion of mean for females or for "small-toothed" group (i.e. *S. brownei*) in *Sthenurus*.

† Data from Sharman, Frith and Calaby, 1964.

TABLE 6

Tooth dimensions in specimens of *Sthenurus brownei* from Strong's Cave and Wanneroo, Western Australia.

Length x width, upper permanent premolar; side			
66.11.62 Strong's Cave	c. 14.5 x 12.0;	L	
65.9.59 Strong's Cave	c. 15 x c. 12;	L	
Depth, lower incisor; side			
65.6.45 Strong's Cave	9.0;	L	
65.6.61 Strong's Cave	10.0;	R	
65.6.65 Strong's Cave	9.6;	R	
Length x width, mandibular cheek teeth; side			
61.11.64 Strong's Cave	P ₃ c. 8.6 x c. 7.6;	L	
61.11.63 Strong's Cave	P ₄ c. 14.6 x c. 10.2;	L	
65. 9.28 Strong's Cave	M ₂ 10.4 x 9.5;	R	
65. 9.28 Strong's Cave	M ₃ 11.0 x 9.9;	R	
61. 6. 2 Wanneroo	P ₃ 8.3 x 7.5;	R	
61. 6. 2 Wanneroo	DP ₄ 8.6 x 8.3;	R	
61. 6. 2 Wanneroo	P ₄ 15.2 x 9.6;	L (excavated)	
61. 6. 2 Wanneroo	M ₁ 10.0 x 8.8;	R	
61. 6. 2 Wanneroo	M ₂ 11.6 x 9.9;	R	
66.10.14 Wanneroo	P ₄ 13.5 x 8.6;	R (excavated)	
66.10.14 Wanneroo	M ₁ c. 9.6 x c. 8;	L	
66.10.14 Wanneroo	M ₂ 10.8 x 9.4;	L	
66.10.14 Wanneroo	M ₃ 11.5 x 10.1;	L	
66.10.14 Wanneroo	M ₄ c. 11 x 9.8;	R	

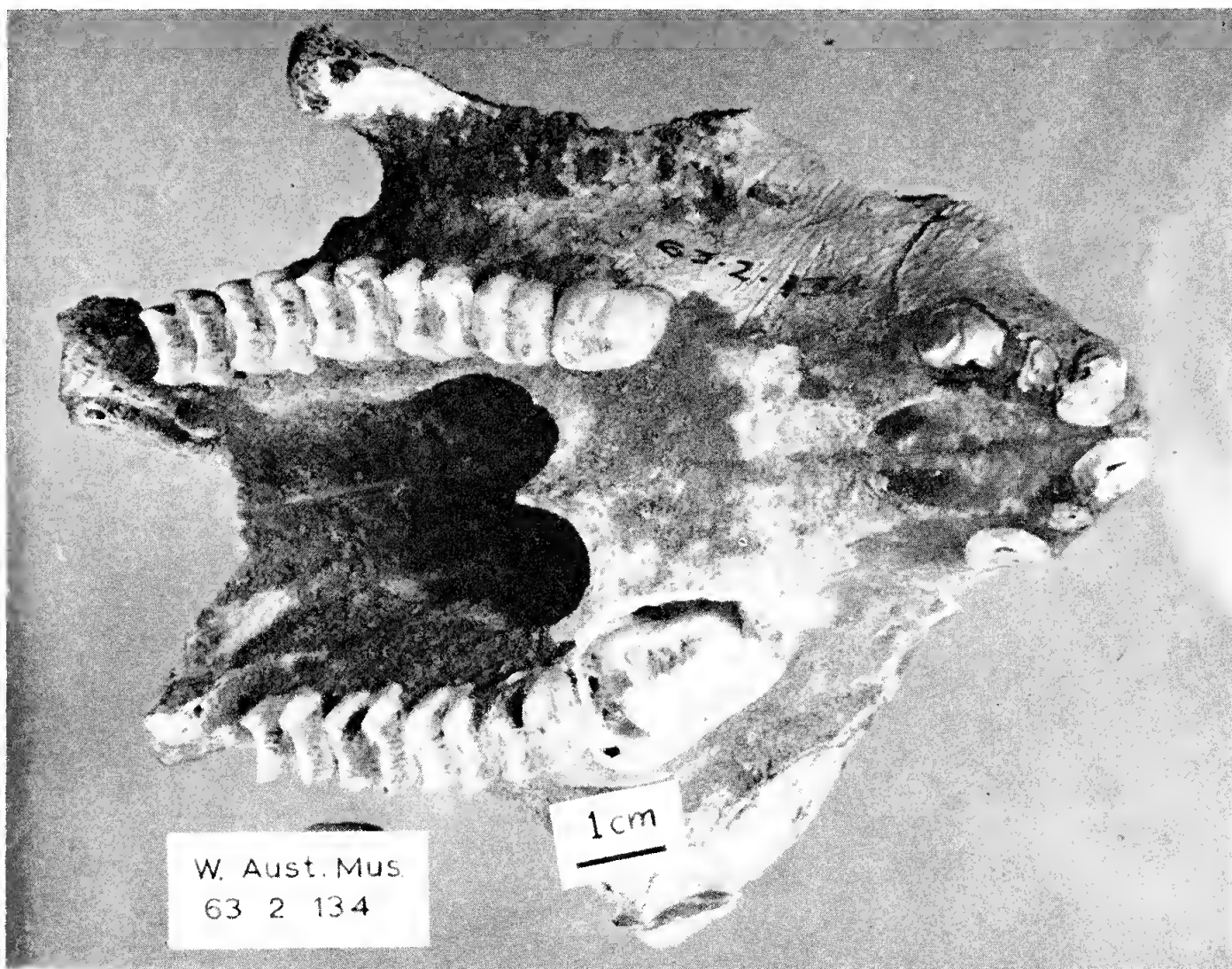


Fig. 7.—Part of skull of *Sthenurus occidentalis*, Mammoth Cave, Western Australia. Left permanent premolar exposed by removing deciduous premolar and milk molar. Compare with *S. brownei*, Fig. 6. Note difference in form of incisive foramina, and difference in forward extent of palatal vacuities.

Thus I conclude that the observed differences between the two groups of *Sthenurus* in Mammoth Cave far exceed sex differences demonstrable in any macropod, or indeed in any mammal sample known to me. A fuller account of the investigations upon which this conclusion is based is given elsewhere (Merrilees, Ph.D. dissertation). If the observed differences within the Mammoth Cave sample are not sex differences, the only other reasonable postulate is that they are specific differences.

Subgeneric status of *S. brownei* and *S. occidentalis*

Tedford (1966) suggests that subgeneric distinction should be made between species with procumbent lower incisors, narrow, trenchant premolars, narrow molars etc. (such as *S. atlas*) and species with incumbent lower incisors, massive premolars, wide molars etc. (such as *S. orientalis*). Both *S. occidentalis* in the revised sense and *S. brownei* fall into the latter group, for which Tedford proposes the subgeneric name *Simosthenurus*.

Sthenurus in Strong's Cave

Strong's Cave is in the same series of calcareous aeolianites as Mammoth Cave, but about 7 miles further south. Cook (1963) suggests

that the Strong's Cave fauna is younger than that of Mammoth Cave, and I have shown (Merrilees, Ph.D. dissertation) that the Strong's Cave fossiliferous deposits may be younger than those of Mammoth Cave.

W. Aust. Mus. specimen 61.11.10 is one of several *Sthenurus* specimens recovered from the bed of a stream traversing Strong's Cave (Cook 1963); it is a left lower permanent premolar with a fully formed crown and portions of the roots, from which the posterior roots and part of the crown have been removed by stream erosion. Its length cannot be recorded with certainty, but is about 15.9 mm; its width is 10.2 mm. Thus it is shorter than any Mammoth Cave specimen of *S. occidentalis* and longer than any Mammoth Cave specimen of *S. brownei*. However, it closely resembles the Mammoth Cave sample of *S. occidentalis* in form, and in spite of its shortness, I ascribe it to *S. occidentalis*. It is the only specimen of this species so far recovered from Strong's Cave.

On the other hand, several specimens from Strong's Cave, though all fragmentary, are referable with confidence to *S. brownei*; these are 61.11.62-63, 65.6.45, 65.6.61, 65.6.65, 65.9.28, 65.9.59. See Table 6. Specimens 61.11.64, 65.6.58 and 65.6.63 are probably *S. brownei*, while

various other fragmentary specimens (e.g. 65.9.96), obviously of *Sthenurus*, cannot be specifically identified.

S. brownei from Wanneroo

Two pieces of bone-bearing granular calcareous material were presented to the Western Australian Museum in 1937 by Mr. A. Skroza. The locality from which these specimens came appears not to have been investigated nor even recorded in detail; however, it is known to have been a limestone quarry in the Wanneroo district, on the northern outskirts of the Perth metropolitan region. The specimens can be assumed, therefore, to have come from the aeolianite series informally known as the Coastal Limestone. One of the lumps has been subjected to acetic and monochloroacetic acid treatment, and shown to contain numerous bone fragments, including two different macropodids and possibly a small reptile; so heterogeneous a material may represent an old cave fill cut into by quarry operations. The Coastal Limestone itself is generally considered to be of late Pleistocene age (Smith 1963), and cave deposits within it may be considerably younger; it is therefore safe to assume that the Wanneroo specimens are of late Quaternary age.

The Wanneroo specimen now catalogued as 61.6.2 shows the central portions of right and left mandibular rami of a juvenile *Sthenurus*, almost certainly two sides of the same mandi-

ble. It was identified as *S. occidentalis* by L. Glauert in 1937, but I have extracted the unerupted permanent premolar from the left side and this shows it to be *S. brownei*. The molars and milk molars in this specimen are consistent in morphology and size with the Mammoth Cave sample of *S. brownei*, but the deciduous premolars are shorter. The excavated left permanent premolar shows a small supernumary root on the lingual side between the large anterior and posterior roots.

Acid preparation of the other Wanneroo lump has revealed a mandible (66.10.14) with the two rami still in contact, very little distorted from the life position. It lacks both incisors, the coronoid and condylar regions of both sides, and the deciduous premolars and milk molars of both sides, the unerupted permanent premolars both being exposed. The first three molars of the right side are extensively damaged. See Figure 8. In form, the permanent premolars, the molars, and the masseteric crest are very similar to the Mammoth Cave sample of *S. brownei*, and the length of the permanent premolar and the first three molars, and the widths of the second and third molars fall within the range of variation of the Mammoth Cave sample. However, the permanent premolar and the first molar are narrower than in any Mammoth Cave specimen of *S. brownei*, and the fourth molar is both narrower and slightly shorter. See Table 6.

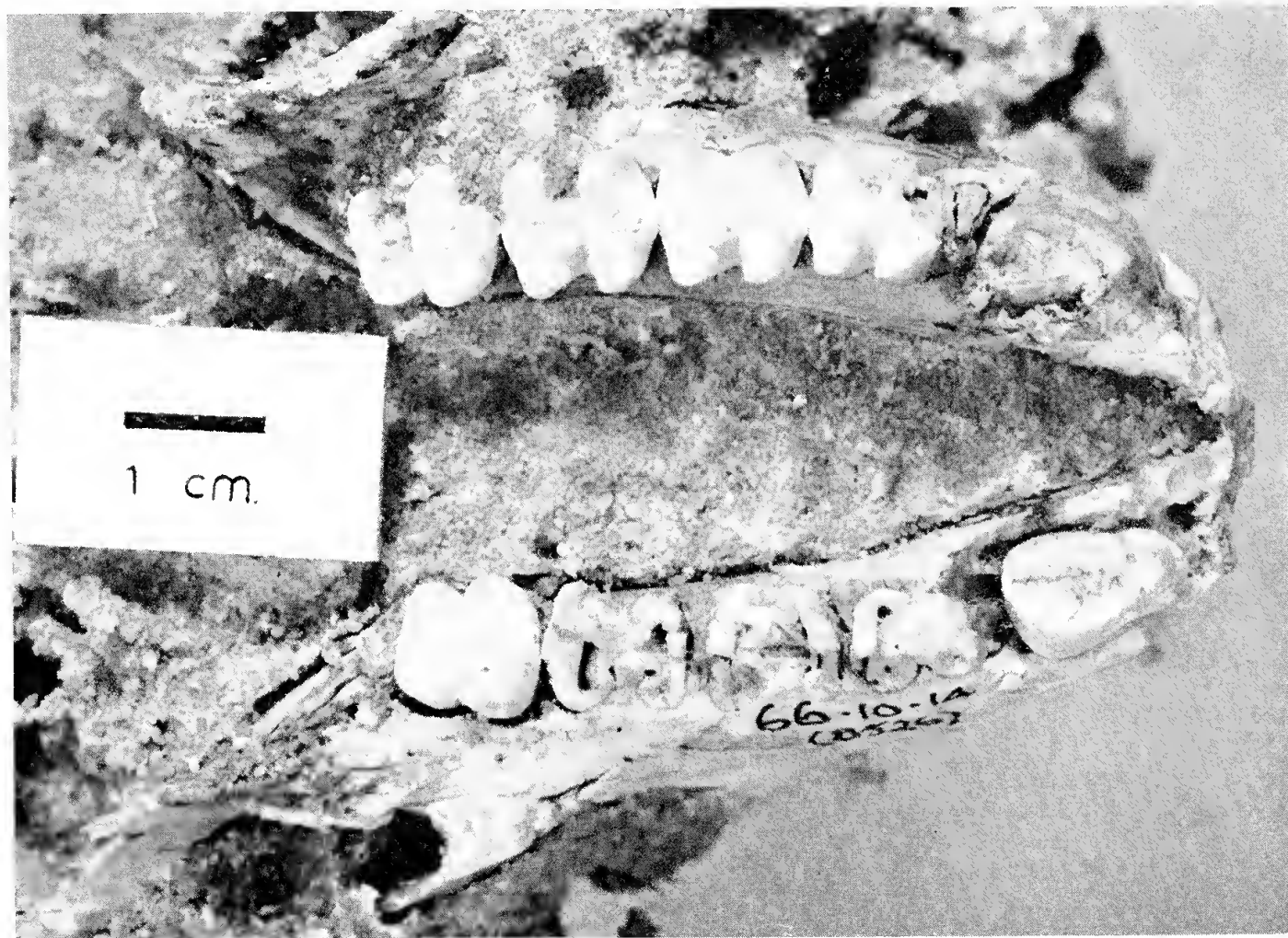


Fig. 8.—*S. brownei* from Wanneroo, near Perth. W. Aust. Mus. 66.10.14.

I conclude that *S. brownei* once lived at Wanneroo, but that there may have been some tendency to smaller teeth in the Wanneroo than in the Mammoth Cave populations.

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10.—The genus *Vermicella* (Serpentes, Elapidae) in Western Australia and the Northern Territory

by G. M. Storr*

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Abstract

The concept of *Vermicella* is enlarged so as to embrace all Australian "coral snakes" and "bandy-bandies", thus causing *Rhynchoelaps*, *Brachyuropsis* etc. to fall into synonymy. Six species (*annulata*, *bertholdi*, *calonotos*, *bimaculata*, *fasciolata* and *semifasciata*) are dealt with and an additional seven subspecies, three of which are new: *annulata snelli*, *bertholdi littoralis* and *semifasciata incincta*.

Introduction

The seven species of Australian coral snakes and bandy-bandies were described between 1841 and 1884. In the same short period seven generic names were proposed for them, not counting the numerous genera, colubrid as well as elapid, in which authors wrongly placed them.

Boulenger (1896) brought some order to the group by reducing the number of genera to two, *Furina* and *Rhynchelaps*. But his choice of names for the genera was inept (as was his allocation of the species). As originally conceived (Duméril 1853: 517) *Furina* was composite, and only *F. diadema* (Schlegel) of its four included species was not a *nomen nudum*. Thus the designation by Jan (1859: 124) of *diadema* as type-species of *Furina* was well founded. This action (which incidentally made *Furina* an objective synonym of *Brachysoma* Fitzinger) was ignored by Günther (1863: 24) when he chose *F. bimaculata* as type-species of *Furina*. In this he was followed by Boulenger who included *bimaculata* in his concept of *Furina* but not *diadema*. The name of Boulenger's other genus was an emendation of the *nomen nudum* *Rhynchoelaps* Jan, which even its proposer had forgotten when describing its type-species, *bertholdi*, a few months later.

Recently, Kinghorn (1955) has split one of Boulenger's genera (*Rhynchelaps*) into three virtually monotypic genera, and Worrell (1960, 1961) has done likewise with the other. To show how little reliance can be placed on these "genera", Kinghorn put *approximans* in *Rhinelaps* with *fasciolata*, rather than in *Brachyuropsis* with the other races of *semifasciata*. Similarly Worrell put *minima* in *Melwardia* with *calonotos*, rather than in *Rhynchoelaps* with the other races of *bertholdi*.

Despite some diversity in coloration and the degree to which they are modified for burrowing, these snakes clearly form a chain of closely related species. When they are brought together, the resultant genus *Vermicella* is no less homogeneous than other Australian genera of Elapidae.

In contrast to the past generic confusion, the species have generally presented workers with little difficulty. The morphological gaps between them are of a considerably higher order than those between the races of any species; and almost all taxa can be recognised on coloration alone. Next in importance for diagnosis are the ventrals, subcaudals and lateral head shields

(temporals, preocular, nasal and labials). The upper head shields (except in one instance for internasals) are of little value; they have been described mainly in order to refute the reliance placed on them by previous workers. The scutellation of the lower jaw is of even less value and has not been described here; details of lower labials, chin-shields etc. are available on request.

The present study is based mainly on specimens in the Western Australian Museum; their numbers are prefixed with R only. For the loan of specimens in the collection of the Northern Territory Administration, Alice Springs (numbers prefixed with NTM); in the South Australian Museum, Adelaide (SAM); National Museum, Melbourne (NM); Australian Museum Sydney (AM); and Queensland Museum, Brisbane (QM); I am indebted respectively to Messrs B. Hart, F. J. Mitchell, J. McNally, H. G. Cogger and J. T. Woods. I am grateful to Mrs. A. Neumann (Librarian, Western Australian Museum) for translating Sternfeld's description of *Rhynchelaps anomalus*.

Genus *Vermicella* Günther

- Vermicella* Günther, 1858: 236. Type-species (by monotypy): *V. annulata* (Gray).
Homaloselaps Jan, 1858: 518. Type-species (by monotypy): *Elaps occipitalis* Duméril, Bibron & Duméril [= *V. a. annulata*]. [*Nomen nudum*.]
Rhynchoelaps Jan, 1858: 518. Type-species (by monotypy): *Elaps bertholdi* Jan. [*Nomen nudum*.]
Simoselaps Jan, 1859: 123. Type-species (by monotypy): *Elaps bertholdi* Jan. [(?) *Nomen nudum*.]
Brachyuropsis Günther, 1863: 21. Type-species (by monotypy): *B. semifasciata* Günther.
Neelaps Günther, 1863: 24. Type-species (by monotypy): *N. calonotos* (Duméril, Bibron & Duméril).
Rhinelaps Günther, 1872: 33. Type-species (by original designation): *R. fasciolatus* Günther.
Rhynchelaps Boulenger, 1896: 361. Emendation of *Rhynchoelaps* Jan.
Hornea Lucas & Frost, 1896: 150. Type-species (by monotypy): *H. pulchella* Lucas & Frost [= *V. fasciolata fasciata* Stirling & Zietz].
Melwardia Worrell, 1960: 132. Type-species (by original designation): *M. minima* Worrell [= *V. bertholdi anomala* (Sternfeld)].
Naropsis Worrell, 1961: 27. Type-species (by monotypy): *N. bimaculata* (Duméril, Bibron & Duméril).

Diagnosis.—Small short-tailed elapid snakes with 15 or 17 rows of smooth scales, divided anal and subcaudals, and more or less prominent snouts. Distinguished from *Aspidomorphus* and *Glyphodon* by smaller head (not wider than neck), more prominent snout (rostral extending back at least quarter way to frontal), shorter and less dentigerous maxillary, and smaller post-frontal. Distinguished from *Demansia* by having no "canthus rostralis", eye much smaller than its distance from mouth, supraocular much smaller than frontal, subcaudals fewer than 36, shorter and less dentigerous maxillary, and exclusion or near exclusion of frontals from orbit.

Distribution.—Australia between latitudes 12 and 38° S.

Description.—Body slender to moderately stout. Tail 4-16% of total length, relatively longer and slenderer in males than females. Snout moderately or greatly prolonged past mouth, its tip rounded or acute in profile.

* Western Australian Museum, Perth, Western Australia.

The nine colubroid upper head shields are only occasionally fused and seldom divided. Rostral always visible from above; its apex either rounded, obtusely angular or acute, and reaching back $\frac{1}{4}$ - $\frac{3}{8}$ way to frontal. Internasals smaller than prefrontals and, except in one race of *annulata*, not normally fused to them. Prefrontal-internasal suture transverse or oblique (backwards to midline of head). Frontal much larger than supraoculars. Parietals varying from short and wide to long and narrow.

Nasal entire (semidivided in some races of *semifasciata*) and normally contacting preocular (except in *warro* and *fasciolata*). Postoculars 2, lower usually smaller and sometimes fused to an adjacent shield. Temporals basically 1 + 1 + 2, but fusion common (especially between primary and secondary); division rare (except in *warro*, where 2 + 2 + 3 is normal).

Upper labials normally 5 or 6, last longest, third and fourth entering orbit. Lower labials normally 7, fourth largest, last smallest. Chin-shields small, anterior pair contacting first three labials and occasionally fourth; posterior pair usually a little longer and narrower than anterior, completely or partly separated by azygous or paired scales, normally in broad contact with fourth labial and often narrowly with third.

Dorsal scales smooth, 15 or 17 rows, increasing (if at all) only on neck and reducing (if at all) immediately or a little before vent. Anal and all subcaudals normally divided (except in some races of *bertholdi*, which commonly have first few subcaudals entire).

Upper surface white, yellow or reddish, variously marked with black or dark brown. Common to all taxa is a dark blotch on nape, and to all but *warro* and some races of *bertholdi* a dark blotch on head (frontals, parietals, temporals, down to at least level of eyes). Many snakes have end of snout dark and body and tail crossed or encircled by numerous dark bands. Remaining taxa unbanded, including one with dark vertebral stripe.

Key to western taxa

- (1) Scale rows 15 2
- Scale rows 17 10
- (2) Body and tail banded 3
- Body and tail not banded 8
- (3) Bands black, usually encircling body; snout not upturned and not tipped with cutting edge 4
- Bands dark brown, not reaching lower surface; snout upturned and tipped with cutting edge *semifasciata roperi*
- (4) Dorsal ground colour white; nasal not lower than long; ventrals more than 240 5
- Dorsal ground colour yellow; nasal much lower than long; ventrals fewer than 140 6
- (5) Internasals fused to prefrontals *annulata multifasciata*
- Internasals free *annulata snelli*
- (6) Upper labials 6 (excluding primary temporal if it reaches lip); head blotch absent or small and ill-defined 7
- Upper labials 5 (excluding primary temporal which reaches lip); head blotch large and sharply defined *bertholdi anomala*

- (7) Occipital bar of black-edged, white-centred scales, ill-defined from head and nuchal blotches; nuchal blotch more than 4 scales long; dark lines along throat; primary temporal not reaching lip *bertholdi bertholdi*
- Occipital bar white, sharply defined from head and nuchal blotches; nuchal blotch not more than 4 scales long; no lines along throat; primary temporal usually reaching lip *bertholdi littoralis*
- (8) Primary temporal large and square, broadly contracting lip *bertholdi anomala*
- Primary temporal low and oblong, distant from lip 9
- (9) Vertebral stripe of black-edged white-centred scales; upper labials 6; ventrals fewer than 150 *calonotos*
- No vertebral stripe; upper labials normally 5; ventrals more than 170 *bimaculata*
- (10) Preocular widely separated from nasal, contacting frontal or narrowly separated 11
- Preocular contacting nasal (abnormally narrowly separated), widely or narrowly separated from frontal 12
- (11) Nuchal blotch more than 6 scales long; bands undulate in pattern, less than one scale wide at midbody *fasciolata fasciolata*
- Nuchal blotch less than 6 scales long; bands reticulate in pattern, more than one scale wide at midbody *fasciolata fasciata*
- (12) Body and tail banded 13
- Body and tail not banded *semifasciata incincta*
- (13) Apex of rostral not sharper than right-angle; midbody bands 5 or more times as wide as pale interspaces *semifasciata approximans*
- Apex or rostral much sharper than right-angle; midbody bands 4 or fewer times as wide as pale interspaces 14
- (14) Upper labials 5; nasal entire; primary and secondary temporals often fused *semifasciata semifasciata*
- Upper labials normally 6; nasal semidivided; temporals seldom fused *semifasciata roperi*

Vermicella annulata multifasciata (Longman)

Furina multifasciata Longman, 1915:30. Darwin, Northern Territory (G. F. Hill).

Diagnosis.—The species *V. annulata* (Gray) is recognised by its elongate body boldly banded with black and white. Present race distinguished from others by fusion of internasals with prefrontals; further distinguished from *V. a. annulata* by more numerous ventrals, and from *V. a. snelli* by narrower bands separated by narrower interspaces.

Distribution.—Far northwest of Northern Territory from Darwin southeast to Pine Creek, and far northeast of Western Australia at Turkey Creek.

Description.—Snout rounded in profile. Total length: males 316-535, females 317-423. Tail (% total length): males 5.1-6.9, females 4.1-5.0.

Rostral wider than high, apex reaching back 0.25-0.4 way to frontal. Internasals fused with prefrontals. Frontal 1.5-1.9 times as long as wide, 0.6-0.8 as long as parietals, and 1.5-2.2 as wide as supraoculars. Nasal a little higher than long, broadly contacting large preocular which is usually separated from frontal. Postoculars 2, lower smaller. Temporals usually 1 + 1 + 2, primary much the largest. Upper labials 6.

Scale rows 15, usually increasing on neck (usually to 17, occasionally 16), not reducing before vent. Ventrals: males 254-265, females 270-282. Subcaudals: males 20-24, females 18-20.

End of snout (i.e. upper surface of rostral) black. Head blotch black, beginning just before frontal and usually finishing just before end of parietals and extending down over last two labials to lips. Nuchal blotch black, 6-9 scales long and separated from parietals by $\frac{1}{4}$ -1 vertebral scales. Back crossed by 46-74 black bands in males (54-83 in females), usually encircling body but apt to be narrower on sides and paler below, $2\frac{1}{4}$ -4 scales wide at midbody and separated by white interspaces $\frac{3}{4}$ -1 $\frac{1}{2}$ scales wide. One specimen (R 10476) with bands broken underneath has midventral line of dark spots. Tail with 4-7 black rings. Prefrontal bar, occipital bar and throat white or pale brownish grey. Black markings fading to brown in alcohol.

Remarks.—For a photograph of holotype and drawings of its head, see Waite & Longman (1920).

Material.—**Western Australia:** Kimberley Division: NM D 4716 (Turkey Creek, 107 mi. S of Wyndham). **Northern Territory:** QM J 2019 (holotype), R 8687, R 10476, NTM 1078, NTM 2662 (Darwin); R 26225 (Parap, suburb of Darwin); R23205 (Harriet Creek, 16 mi. NE of Pine Creek).

Vermicella annulata snelli subsp. nov.

Holotype.—R 19203 in Western Australian Museum, an adult female collected by C. Snell early in 1963 at Mundiwindi, Western Australia, in 23° 51' S, 120° 09' E.

Diagnosis.—Distinguished from *V. a. multifasciata* by free internasals, and from *V. a. annulata* by more numerous ventrals (254-313, against 180-243).

Distribution.—Pilbara region of Western Australia, south to Hamersley Range and east to Marble bar and Mundiwindi; and Northern Territory at Roper River Mission and in southern highlands.

Description.—Total length: males 262-452, females 271-504. Tail (% total length): males 4.6-6.0, females 4.2-4.6.

Rostral wider than high, apex reaching back 0.3-0.45 way to frontal. Suture between internasals 0.3-0.8 times as long as suture between prefrontals. Frontal 1.5-2.3 times as long as wide, 0.6-0.9 as long as parietals, and 0.9-2.5 as wide as supraoculars. Nasal a little higher than long, broadly contacting preocular which is moderately or widely separated from frontal. Postoculars usually 2, lower smaller and occasionally fused to upper or to temporal. Temporals normally 1 + 1 + 2, primary much the largest and occasionally fused to fifth labial. Upper labials 6.

Scale rows 15, usually increasing on neck (usually to 17, occasionally 16 or 18), usually not reducing before vent. Ventrals: males 259-289, females 264-313. Subcaudals: males 20-26, females 17-21.

End of snout (i.e. internasals and upper surface of rostral) black. Head blotch black, beginning on or just before frontal, finishing about end of parietals, and extending down over last two labials to lips. Nuchal blotch black, 6-9 scales long, separated from parietals by $\frac{1}{2}$ -2 vertebral scales. Back crossed by 34-66 black bands, usually encircling body, $3\frac{3}{4}$ -5 $\frac{1}{2}$ scales wide at midbody and separated by white interspaces $1\frac{1}{2}$ -3 scales wide. Specimens with incomplete bands may have a midventral line of dark spots interrupted opposite bands. Tail with 3-6 black rings.

Geographic variation.—The material comes from three widely disjunct regions. The Pilbara series is the most distinctive and is characterised by (1) high ventral counts (averaging 284 in males, and 305 in females); (2) strong rostral—it is almost as high as wide and its angular apex extends back at least $\frac{2}{3}$ of way to frontal (in Northern Territory specimens the apex is rounded and extends back not more than $\frac{1}{3}$ of way to frontal); and (3) large head blotch—it usually extends a little past end of parietals (whereas in the Territory it usually finishes a little before end of parietals) and in half of the series it extends forward along midline to snout patch. Within the Pilbara series, the Mt. Herbert and Tambrey specimens are notable for their numerous body bands, viz. 55 and 66, against 34-41 for all other specimens of the race.

The Roper River series is characterised by low ventral and subcaudal counts and narrow frontal. The Central Australian specimens are notable for their wide frontal, especially as compared with width of supraoculars.

Remarks.—This snake is named after Mr Charles Snell who donated the holotype to the Western Australian Museum and many other reptiles from the upper Ashburton, Ophthalmia Range and Mundiwindi district.

Paratypes.—**Western Australia.** *North-West Division:* R 439 (Marble Bar); R 20238 (Mt. Herbert, 40 mi. S of Roebourne); R 6745 (Tambrey); R 17122 (Wittenoom); R 19204 (Mundiwindi). **Northern Territory:** NM D 10072-4 (Roper River Mission); NTM 75, NTM 2577 (Alice Springs); NTM 76 (Hermannsburg).

Vermicella bertholdi bertholdi (Jan)

E[laps] Bertholdi Jan, 1858 : 518. "Ile Adélaïde (Australie méridionale)." [Nomen nudum.]

Elaps Bertholdi (Simoselaps) Jan, 1859 : 123.

No locality [= Perth, Western Australia].

Furina robusta De Vis, 1905 : 51. Coolgardie, Western Australia (R. L. Reid).

Diagnosis.—The species *V. bertholdi* is recognised by its yellow dorsum boldly banded with black. Present race distinguished by poorly defined occipital bar of black-edged, white-centred scales and by dark lines along throat and side of fore-neck (formed by darkening of lateral edges of scales).

Distribution.—Lower west coast and coastal plain of Western Australia from Gingin south to Bunbury, and in the interior from Marilla, Ullawarra and Mundiwindi south to Kojonup, Hyden and the Eastern Goldfields, east into western South Australia and extreme south of Northern Territory.

Description.—Snout depressed, angular in profile but not tipped with cutting edge. Total length: males 102-254, females 89-301. Tail (% total length): males 10.7-13.1, females 7.8-9.7.

Rostral much wider than high, apex obtuse and reaching back 0.2-0.4 way to frontal. Suture between internasals 0.6-1.8 times as long as suture between prefrontals. Frontal 1.7-2.5 times as long as wide, 0.6-0.8 as long as parietals, and 1.4-2.2 as wide as supraoculars. Nasal long and low, contacting preocular which is widely or narrowly separated from frontal. Postoculars 2, lower usually smaller. Temporals 1 + 1 + 2, primary descending well down between fifth and sixth labials but never entirely separating them; upper tertiary large, especially when fused to scale behind it. Upper labials 6.

Scale rows 15, nearly always increasing on neck (usually to 17, occasionally 16), and always reducing before vent (usually to 13, sometimes 11, 12 or 14). Ventrals: males 112-127, females 118-131. Subcaudals: males 19-25, females 15-20.

Head creamy or olive grey, anteriorly freckled with black, posteriorly blotched with black (mainly on parietals and temporals). Occipital bar $\frac{1}{2}$ -3 vertebral scales wide; scales white, narrowly or widely edged with black; obscurely demarcated from parietal and nuchal blotches. Nuchal blotch black, $4\frac{1}{2}$ -7 $\frac{1}{2}$ scales long, usually encircling neck but narrower underneath. Body with 15-25 black rings (except for an Ernabella female with 32), occasionally broken midventrally, $1\frac{3}{4}$ -3 $\frac{3}{4}$ scales wide at midbody (narrower in males than females) and separated by yellow interspaces 2-4 $\frac{1}{2}$ scales wide (narrower in males than females). Tail with 3-6 black rings (more in males than females). Dorsal ground coloration yellow, the scales edged with orange-red (except on two rows next to ventrals). Throat olive grey, anteriorly freckled with black; posteriorly (as on side of fore-neck) scales laterally edged with dark brownish grey so as to form narrow longitudinal stripes. Occasional specimens have dark midventral blotches between annuli.

Geographic variation.—In spite of its very wide range and some gaps in its distribution, e.g. Darling Range, this race undergoes little geographic variation. Apart from local peculiarities (some of which are mentioned below), variation is restricted to a few weak clines. From southwest to north and east the following changes occur:

- (1) absolute size increases—maximum attained at Ernabella in far northeast,
- (2) relative length of tail increases,
- (3) ventrals increase—maximum attained at Ullawarra and Middalya in far northwest (males have 3-4 more than elsewhere),
- (4) subcaudals increase,
- (5) dorsal and caudal bands increase,
- (6) width of yellow space between black bands decreases.

Other clines change direction. Length of nuchal blotch, least at Moora and Watheroo, increases towards north and east, but in far northeast it is again small. Similarly, width of bands at first increases north and east from the coastal plain, but decreases in far northeast. This last factor, coupled with no. 6 above, has

the following consequence: all snakes from the Eastern and Murchison Goldfields and some from the far eastern Wheat Belt have the bands wider than the interspaces (which of course does not suffice for the recognition of "robusta").

The Ernabella (S.A.) and southern Wheat Belt (W.A.) populations have a high frequency of individuals with midventral blotches between annuli; it is strange that this trait should be commonest at the southwestern and north-eastern extremities of the taxon's range. The specimen from Ullawarra is notable for the extensive break in its body bands.

Remarks.—Jan & Sordelli's drawing of *Elaps bertholdi* clearly depicts a specimen of the present taxon. The type, according to Jan, had 114 ventrals and 22 subcaudals, which agrees closely with males from Perth. Indeed it is highly improbable that specimens of *V. b. bertholdi* were available in Jan's time from outside of Perth.

For corrections to the original description of *Furina robusta*, see Mack & Gunn (1953 : 66).

Material.—**Western Australia.** *North-West Division:* R 5041 (Marilla); NM R 11016, NM R 11216-7 (Middalya); R 25258 (21 mi. NNW of Ullawarra); R 12277 (Mundiwindi); R 24839 ("Carnarvon"); R 3326 (Landor); R 1422 (Mt. Magnet). *Eastern Division:* R 26412 (25 mi. SW of Wiluna); R 6430 (Gidgee, 35 mi. NNE of Sandstone); R 12402, R 14916 (Kathleen Valley); R 199, R 4311, R 22866 (Kalgoorlie); R 24023 (Dedari, W of Bullabulling), R 22658 (Southern Cross); R 26278-9 (Noongaar). *South-West Division:* R 26642 (22 mi. NE of Yuna); R 19185 (Mullewa); R 26335 (Greenough); R 1552 (Irwin); NM D 9838 (Mingenew); R 9341 (Arrino); R 25612 (Morawa); R 7278 (Caron); R 26404 (Bunjil); R 21875, R 26406 (Maya); R 25283 (15 mi. W of Watheroo); R 9261 (Dandaragan); R 19738-9 (Moora); R 19881 (Kalannie); R 24985 (Mollerin); R 6544 (Wialki); R 1505-6, R 6013 (Koorda); R 1299, R 21566 (Trayning); R 7855 (Mangowine); R 3877-8 (15 mi. N of Lake Brown); R 8581, R 18503, R 24865 (Merredin); R 13452, R 25085 (Kellerberrin); R 14140 (Tammin); R 644 (Beverley); R 2496 (Quairading); R 3390 (Kwolyin); R 5196 (Erikin); R 1157, R 25909 (Narembeen); R 19882 (Corrigin); R 21467-8 (Tutanning Reserve); R 434, R 795, R 4656 (Pingelly); R 13032 (Popanyinning); R 4368-9 (Wandering); R 25976 (Crossman); R 4957 (East Wickepin); R 4320, R 19746, R 21565 (Kulin); R 3429 (King Rocks, 20 mi. ENE of Hyden); R 519-20 (Dulbinning, E of Narrogin); R 25607 (Dudin); R 5367 (Kukerin); R 46 (South Katanning); R 8457 (Gingin); 27 specimens from Perth and suburbs (from Marmion Beach, Tuart Hill and Bassendean south to South Fremantle and Mt. Pleasant); R 19496 (Naval Base); R 13803 (Armada); R 19824, R 21246, R 24908 (Mandurah); R 18604, R 22287 (Miami); R 15107 (Bunbury). *Eucla Division:* R 319 (Balladonia). **South Australia:** NM D 10899-10901 (Ernabella); NM D 1954-5 and 1958 (Oodnadatta); NM D 4661 (Ooldea); SAM R 4734 (The Twins HS); SAM R 2301 (Kingoonya); SAM R 1690 (Bookaloo); SAM R 2118 (Pygery); SAM R 3661 (Kyancutta). **Northern Territory:** R 24471 (Kulgera).

***Vermicella bertholdi littoralis* subsp. nov.**

Holotype.—R 12770 in Western Australian Museum, an adult male collected by Mr Ross Vollprecht on January 16, 1958, in coastal dunes 7 miles south of Geraldton, Western Australia, in 28° 52' S, 114° 38' E.

Diagnosis.—Distinguished from *V. b. bertholdi* by large primary temporal usually reaching lip, sharply defined white occipital bar, nuchal blotch 4 or fewer scales long, and absence or feeble development of dark lines along throat and side of fore-neck.

Distribution.—Mid-west coast of Western Australia from Point Cloates south to Jurien Bay, including Shark Bay islands (Bernier, Dorre and Faure) and Houtman Abrolhos (East and West Wallabi).

Description.—Total length: males 110-199, females 104-385. Tail (% total length): males 11.7-14.2, females 8.0-10.4.

Rostral much wider than high; apex obtusely angular, reaching back 0.3-0.45 way to frontal. Suture between internasals 0.7-1.8 times as long as suture between prefrontals. Frontal 1.45-1.9 times as long as wide, 0.45-0.7 as long as parietals (longer in males than females), and 1.4-2.4 as wide as supraoculars. Nasal contacting preocular which is narrowly separated from frontal. Postoculars 2, lower usually much smaller. Temporals 1 + 1 + 2, primary very large and usually contacting lip. Upper labials 6.

Scale rows 15, increasing on neck in 63% of specimens (to 16 or 17), and reducing to 13 before vent (except in R 4501). Ventrals: males 104-113, females 114-125. Subcaudals: males 20-23, females 16-21.

Head anteriorly freckled with black and posteriorly blotched with black (anterior margin of blotches irregular; posterior margin a sharp transverse line behind parietals). Occipital bar white, 1½-2 scales wide, sharply demarcated from head and nuchal blotches. Nuchal blotch black, 2½-4 scales long (shorter in males than females), usually broken underneath. Body with 16-34 black rings (some not extending to flanks), 1¼-2¾ scales wide at midbody (narrower in males than females) and separated by interspaces of 1¾-3½ scales (narrower in males than females). Tail with 4-8 black rings (more in males than females). Throat suffused with olive grey.

Geographic variation.—The material falls into two groups: a northern from Point Cloates to Shark Bay, and a southern from the Abrolhos to Jurien Bay. Northern snakes differ from southern in having

- (1) only 16-22 rings round body, against 24-34,
- (2) on average one less caudal ring,
- (3) longer nuchal blotch,
- (4) relatively longer tail,
- (5) fewer ventrals and subcaudals.

Remarks.—Generally *littoralis* forms a nice link between *b. bertholdi* and *b. anomala*. However it has peculiarities of its own, such as the very long parietals (compared to frontal) and the tendency for island females to attain great size (three of five specimens exceed 300 mm, and the longest is also extremely stout).

There is nowhere any indication of gene-flow between *littoralis* and nominate *bertholdi*, des-

pite the evident proximity of the two races at Greenough and Irwin. If they should prove to be sympatric, *littoralis* would have to be raised to a full species, and the way would be open to divide it into a northern and southern race.

Paratypes.—**Western Australia.** *North-West Division*: R 16885 (near Point Cloates); NM R 817 (Shark Bay). *Shark Bay islands*: R 20528-9, R 26732 (Bernier); R 26733 (Dorre); R 23636 (Faure). *Houtman Abrolhos*: R 398 (West Wallabi); R 4501 (East Wallabi). *South-West Division*: R 13317, R 13297, R 26297 (Geraldton); R 1687 (Irwin); R 15104, R 23317 (Green Head, 15 mi. N of Jurien Bay); R 13925 ("Medina"); SAM R 2771 ("Murchison Goldfields").

***Vermicella bertholdi anomala* (Sternfeld)**

Rhynchelaps anomalus Sternfeld, 1919 : 77. Hermannsburg, Northern Territory (M. von Leonhardt).

Melwardia minima Worrell, 1960 : 132. Broome, Western Australia (M. Ward).

Diagnosis.—Distinguished from all other races of *V. bertholdi* by 5 (rather than 6) upper labials and large, well-defined head blotch.

Distribution.—Northwest coast of Western Australia from Derby to Onslow, southeast through Great Sandy Desert to Central Australia.

Description.—Total length: males 186-206, females 96-206. Tail (% total length): males 12.1-13.2, females 9.2-10.4.

Rostral much wider than high; apex obtuse, reaching back 0.3-0.45 way to frontal. Suture between internasals 0.7-3.0 times as long as suture between prefrontals. Frontal with posterior angle very acute (sides tending to be concave), 1.4-2.0 times as long as wide, 0.6-0.8 as long as parietals, and 1.8-2.8 as wide as supraoculars. Nasal contacting preocular which is narrowly separated from frontal. Postoculars 2 or 1, lower much the smaller and occasionally fused to temporal. Temporals 1 + 1 + 2, primary much the largest and broadly contacting lip. Upper labials 5, last largest and widely separated from fourth.

Scale rows 15, increasing on neck to 16 or 17, and reducing before vent to 13. Ventrals: males 119-130, females 123-129. Subcaudals: males 23-27, females 17-21.

Head blotch black, reaching forward to about anterior edge of frontal and back to just beyond end of parietals, often continuous on midline with black patch on end of snout (rostral and internasals), and extending down on side of head to posterior labials and occasionally almost to middle of throat. Nuchal blotch black, 3¼-6¾ scales long, usually encircling neck, separated from head blotch by 1-4 vertebral scales. Body and tail normally banded with black. Dorsal bands 20-31, 1½-2¼ scales wide at midbody and separated by pale interspaces of 2¼-3¼ scales. Tail with 5-8 bands in males, 4-7 in females.

Geographic variation.—Ventral counts are highest in Central Australia, least in West Kimberley. Subcaudal counts are evidently lower in West Kimberley than in the Pilbara and Central Australia.

Remarks.—The holotype of *Melwardia minima* differs from neighbouring females of *V. b. anomala* only in coloration: no annuli, shorter nuchal blotch and wider occipital bar.

Material.—**Western Australia.** *Kimberley Division*: R 1393, R 13815 (Derby); AM R 16494 (holotype of *M. minima*), NM R 819 (Broome); R 3441 (Lagrange). *North-West Division*: R 5105 (De Grey); R 8272-3 (Onslow). *Eastern Division*: SAM R 1766 (Well 37, Canning Stock Route). **Northern Territory**: NTM 74, NTM 77, SAM R 1554, SAM R 2316 (2), SAM R 4792 (Hermannsburg); NTM 2028 (Kathleen Creek, George Gill Range); SAM R 1616 (Finke River).

***Vermicella calonotos* (Duméril, Bibron & Duméril)**

Furina calonotos Duméril, Bibron & Drumeril, 1854 : 1241. "Tasmanie" [in error for Perth, Western Australia].

Diagnosis.—Distinguished from other unbanded 15-scaled *Vermicella* by longitudinal stripe of black-edged, white-centred vertebral scales.

Distribution.—Western Australia: lower west coast and coastal plain from Lancelin south to Safety Bay, inland to Bullsbrook, Caversham, Riverton and East Rockingham; also east of Darling Range at York on the upper Avon.

Description.—Body and tail moderately slender. Head narrow. Snout produced beyond mouth but not tipped with cutting edge. Total length: males 162-260, females 124-284. Tail (% total length): males 13.3-15.4, females 10.1-12.6.

Rostral much wider than high, apex reaching back 0.3-0.45 way to frontal. Internasals markedly smaller than prefrontals (absent in one specimen through fusion partly to nasals and partly to prefrontals). Suture between internasals 0.55-1.2 times as long as suture between prefrontals. Suture between internasal and prefrontal transverse. Frontal 1.2-1.55 times as long as wide, 0.7-0.8 as long as parietals, and 2.5-3.6 as wide as supraoculars. Low posterior extension of nasal nearly always contacting preocular. Preocular contacting frontal (30% of specimens) or narrowly separated. Postoculars 2, lower smaller. Temporals basically 1 + 1 + 2, but primary and secondary fused in 80% of specimens to form narrow shield up to 3 times as long as high; occasionally upper tertiary fused to secondary or to lower tertiary. Upper labials 6, last much the longest. Scale rows 15, increasing on neck in 70% of specimens (to 16 or 17), and reducing immediately before vent in 20% of specimens (to 14, 13 or 12). Ventrals: males 126-139, females 130-143. Subcaudals: males 28-35, females 23-29.

End of snout black, i.e. whole of rostral, part of nasal (sometimes as far back as nostril) and up to half of internasals (backward extent greatest about common suture). Head blotch black, usually beginning slightly behind anterior edge of frontal and finishing slightly beyond parietals, and extending down on sides to below eye but not to lip. Nuchal blotch black, 2½-4½ scales long, separated from head blotch by 2-3 vertebral scales; occasional scales towards rear of blotch may be white-centred. Longitudinal stripe from nuchal blotch to end of tail, consisting of white-centred scales narrowly or broadly margined with black (margin thickest distally). Vertebral stripe varies in development: at one extreme it may encroach broadly on to paravertebral scales and have white centres of vertebrals almost obliterated by thick margin; at other extreme, stripe may be

faint and largely discontinuous (in which case, snake will superficially resemble some specimens of *V. bimaculata*). Remainder of upper surface creamy white, each scale margined narrowly or fairly broadly with salmon pink or orange-red.

Geographic variation.—The unique specimen from east of the Darling Range (R 7330) is peculiar in having 35 subcaudals, i.e. 2 more than any other male.

Material.—**Western Australia.** *South-West Division*: R 26721 (9 mi. NE of Lancelin); R 12605 (Lancelin); R 23827 (Yanchep Beach); R 20681 (Yanchep); R 13439 (Pearce); R 1307 (Wanneroo); 46 specimens from Perth and suburbs, from Sorrento, Mt. Yokine and Caversham south to Cottesloe, Applecross and Riverton; R 25065 (Woodman Point); R 12312 (Naval Base); R 9311 (East Rockingham); R 6888 (Safety Bay); R 7330 (York).

***Vermicella bimaculata* (Duméril, Bibron & Duméril)**

Furina bi-maculata Duméril, Bibron & Duméril, 1854 : 1240. "Tasmanie" [in error for Perth, Western Australia].

Diagnosis.—Distinguished from other unbanded, unstriped 15-scaled *Vermicella* by 5 upper labials, the last broadly contacting fourth.

Distribution.—Western Australia from Greenough, Yalgoo (*vide* Loveridge 1934 : 292) and Cue south to Bunbury, Williams and the Eastern Goldfields, thence east into western South Australia.

Description.—Body and tail slender in males, a little stouter in females. Snout produced well beyond mouth but not tipped with cutting edge. Total length: males 156-390, females 163-446. Tail (% total length): males 8.1-10.3, females 5.6-7.4.

Rostral as high as wide; apex obtuse or rectangular, reaching back 0.5-0.7 way to frontal. Internasals almost as large as prefrontals. Suture between internasals 0.4-2.3 times as long as suture between prefrontals. Suture between internasal and prefrontal slightly to moderately oblique. Frontal 1.0-1.6 times as long as wide, 0.6-0.85 as long as parietals, and 2.4-3.6 as wide as supraoculars. Nasal contacting preocular which is well separated from frontal. Postoculars 2, much smaller than preocular. Temporals basically 1 + 1 + 2, but primary and secondary fused in 92% of specimens to form narrow shield up to 4 times as long as high, and tertiaries usually fused to each other. Upper labials normally 5 (6 in R 5210), last almost as long as first four together.

Scale rows 15. Ventrals: males 176-212, females 197-228. Subcaudals: males 25-30, females 19-23.

Head blotch glossy brownish black, beginning just before or behind anterior edge of frontal, and finishing a little before or behind end of parietals. Nuchal blotch glossy brownish black, 3½-6½ scales long, separated from head blotch by 2½-4½ vertebral scales. Scales of back and tail pale reddish brown narrowly or broadly margined with dark reddish brown (margin broadest distally). A few specimens have trace of vertebral stripe owing to widening of dark margin on vertebral scales, especially on forebody and tail.

Geographic variation.—All but four of our specimens (individually described below) fall into one of two groups, the first occupying the

lower west coast and coastal plain from Green Head south to Bunbury, the other the far north and east (that is generally beyond the Wheat Belt). The latter differs from the coastal group in their

- (1) larger size: maximum length of males 390 (against 335 in coastal snakes), females 446 (against 422),
- (2) shorter tail: males 8.2-8.8% of total length, (against 8.4-10.3), females 5.6-6.2 (6.2-7.4),
- (3) more numerous ventrals: males 204-212 (176-192), females 218-228 (197-214),
- (4) scale rows not increasing on neck (increasing to 16 or 17 in 85% of specimens),
- (5) black spot on end of snout in all specimens (usually smaller when present, but absent in most coastal specimens),
- (6) head blotch larger: nearly always beginning before frontal and usually finishing behind parietals (nearly always beginning on or behind anterior edge of frontals and finishing before end of parietals),
- (7) nuchal blotch a little smaller: $3\frac{1}{2}$ -5 scales long ($4-6\frac{1}{4}$), and separated from head blotch by narrower space: $2\frac{1}{4}$ -4 vertebrae ($3-4\frac{1}{2}$),
- (8) dorsal coloration usually darker, owing to wider scale margins.

In the northwest there has evidently been no recent contact between the two groups, if two males said to come from Greenough really do so. They have 30-36 more ventrals than a male from Green Head (only 77 miles to south). Moreover each of these three specimens is typical of its group with respect to presence or absence of snout spot, extent of head blotch and number of scale rows on neck.

Further south and east, however, there is a broad zone in which individuals variously combine the characters of the two groups. The two specimens from in or near the northeastern Wheat Belt (R 7854, R 4890) agree with the inland group in their short tails and numerous ventrals, but both have 17 scale rows on the neck and the nuchal blotch as in coastal snakes. Moreover R 4890 has no snout spot.

The two other specimens that cannot be assigned to either group are more complex in their admixture of characters and have peculiarities of their own. The male from Wundowie resembles the inland group in its large size (336 mm), dark dorsal coloration (indeed it is darkest of all our *bimaculata*), head blotch extending beyond parietals, and 15 scale rows on neck; but it has only 189 ventrals, a relatively long tail (9.1%), no snout spot, and nuchal blotch 6 scales long. The male from Williams resembles coastal snakes in its pale coloration, extent of head blotch, and number of scale rows on neck (17); but it has 198 ventrals, tail rather short (8.6%), snout black-tipped, and nuchal blotch extremely short ($3\frac{1}{2}$ scales).

It is significant that the character, small head blotch, finds its extreme expression in the very south of the coastal group's range, i.e. in our single specimen from Bunbury, which is also notable for its dusky throat.

Remarks.—At first sight it would appear that an inland race should be recognised, but certain

difficulties preclude their formal separation. First there is the practical task of allocating the four problematic specimens to one or another race. If they had come from a small area or narrow zone it perhaps would not matter much what was done with them, but in fact they jointly occupy a substantial part of the species' range. If races were recognised, one should be able to state unequivocally which of them occurred in, say, the Wheat Belt.

Then there is the theoretical question, are these really races or incipient races or merely the ends of various clines? If the two groups were really races one could dispose of the problematic specimens as hybrids, and indeed the Wundowie specimen and (to a lesser extent) the Williams specimen have in their hotpotch of characters every appearance of being hybrids. But the two other specimens are not so easily disposed of and seem rather to be genuine intergrades.

Despite the inadequacy of our sample, it is clear that we are not dealing here with clines of the sort we noticed in *V. b. bertholdi* and will observe again in *V. s. semifasciata*. Instead we seem to have character plateaux separated by steps. The trouble from the taxonomist's viewpoint is that the several steps are not geographically coincident. Number of ventrals, for example, increases sharply to the immediate east of the Darling Range. In contrast, extent of head blotch after increasing between Bunbury and Perth remains much the same for at least 150 miles to the northeast of Perth.

Material.—**Western Australia.** *North-West Division:* R 719 (Lakeside, 30 mi. SW of Cue). *Eastern Division:* R 4921 (Menzies); R 5210 (Bulong); R 4722 (Kurrawang, 8 mi. SW of Kalgoorlie). *South-West Division:* R 26333-4 (Greenough); R 4890 (Lake Moore, 60 mi. E of Wubin); R 7854 (Mangowine, near Nungarin); R 13885 (Wundowie); R 4708 (Williams); R 23318 (Green Head, 15 mi. N of Jurien Bay); 30 specimens from Perth and suburbs (from Sorrento and Bassendean south to East Fremantle and Kenwick); R 5204 (Gosnells); R 9155 (Bunbury). **South Australia:** SAM R 1791 (Ooldea); SAM R 2302 (Kingoonya).

***Vermicella fasciolata fasciolata* (Günther)**

Rhinelaps fasciolatus Günther, 1872: 34.
Perth, Western Australia (F. H. du Boulay).

Diagnosis.—The species *V. fasciolata* is distinguished from other 17-scaled *Vermicella* by wide separation of nasal from preocular. Present race distinguished by long nuchal blotch and narrow, undulate bands.

Distribution.—Western Australia from Shark Bay and Wiluna south to Perth and Widgiemooltha and east to Laverton (i.e. between latitudes 26 and 33° S, and west of longitude 123° E).

Description.—Body moderately stout. Head broad and somewhat depressed. Snout obtuse in plan, acute in profile, extending well beyond mouth and tipped with moderately sharp cutting edge. Total length: males 139-349, females 156-390. Tail (% total length): males 11.0-13.5, females 7.4-9.1.

Rostral wider than high; apex angular, penetrating slightly or moderately deeply between internasals. Suture between internasals 0.8-4.0 times as long as suture between prefrontals.

Suture between internasal and prefrontal transverse or moderately oblique. Frontal 1.2-1.7 times as long as wide, 0.75-1.2 as long as parietals, and 2.1-3.5 as wide as supraoculars. Nasal widely separated from preocular which contacts frontal (68% of specimens) or is separated (but by never more than half its height). Postoculars 2 (65% of specimens) or 1 (when lower fused to temporal or fifth labial). Temporals normally 1 + 1 + 2, larger than in *V. semifasciata* and seldom fused (primary with secondary in one specimen, and upper with lower tertiary in five). Upper labials 6.

Scale rows 17, increasing on neck to 19 or 21, and nearly always reducing to 15 immediately before vent. Ventrals: males 140-157, females 155-172. Subcaudals: males 24-30, females 19-22.

Head blotch black, extending back to end of parietals or a little before end, and forward nearly to anterior edge of frontal and sometimes narrowly along snout. Nuchal blotch black, 7-15 scales long, either continuous on midline with head blotch or separated by up to 1½ vertebral scales. Back and tail reddish (sometimes greyish in juveniles) narrowly banded with black. Males with 54-83 bands across body and 9-17 across tail, females with 59-85 and 6-11. Bands increasingly broken posteriorly and tending to be merely transverse rows of black U-shaped marks; ½-1 scale wide at midbody, separated by interspaces of ½-2 scales. All black marks fading to dark brown in alcohol, and dorsal ground coloration to creamy white.

Material.—**Western Australia.** *North-West Division:* R 24094 (4 mi. E of Denham). *South-West Division:* R 26502 (22 mi. NE of Yuna); R 402 (Carnamah); R 5936-7 (Jurien Bay); R 23883 (Ledge Point); R 20580 (Regan's Ford, 20 mi. S of Dandaragan); R 16500 (Beacon); R 2864 (Bencubbin); R 4253 (Bullsbrook); R 5939 (Caversham); R 13468 (Morley Park); R 14244 (Double View); R 8389 (Mt. Hawthorn); R 7056 (North Perth); R 25985 (City Beach); R 1311 (North Lake, Melville). *Eastern Division:* R 6323 (Wiluna); R 1751 (Laverton); R 26643 (Widgiemooltha).

***Vermicella fasciolata fasciata* Stirling & Zietz**

Vermicella fasciata Stirling & Zietz, 1893 : 175. Near Barrow Range, Western Australia (Elder Expedition).

Hornea pulchella Lucas & Frost, 1896 : 150. Charlotte Waters, Northern Territory (W. B. Spencer).

Diagnosis.—Distinguished from *V. f. fasciolata* by smaller nuchal blotch and wider body bands (which are reticulate in pattern rather than undulate).

Distribution.—Far east of Western Australia near Warburton, Barrow and Rawlinson Ranges, thence east into far northwestern South Australia and extratropical Northern Territory.

Description.—Maximum length: males 215-310, females 213-340. Tail (% total length): males 12.2-15.3, females 7.7-9.2.

Rostral wider than high, apex reaching back 0.3-0.4 way to frontal. Suture between internasals 0.7-1.5 times as long as suture between prefrontals. Frontal 1.4-1.7 times as long as wide, 0.75-1.0 as long as parietals, and 1.8-2.8 as wide as supraoculars. Nasal widely separated from preocular which is moderately or narrowly separated from frontal. Postoculars 2.

Temporals 1 + 1 + 2, except in one specimen which has 3 tertiaries; another has upper tertiary fused to secondary. Upper labials 6.

Scale rows 17, increasing on neck to 19 or 21, reducing immediately before vent to 15. Ventrals: males 150-156, females 158-172. Subcaudals: males 24-29, females 17-21.

Nuchal blotch 3½-5¾ scales long, separated from head blotch by 1-2½ vertebral scales. Males with 50-60 bands across body and 11-14 across tail; females with 49-73 and 8-10. Bands consisting of pale-centred scales widely margined with black; 1¼-2 scales wide at midbody (wider in males than females), separated by interspaces of 1-1¾ scales. Dark marks fading to purple in alcohol and ground coloration to pale pinkish brown.

Geographic variation.—The Northern Territory specimens differ from the Western Australian in having a relatively shorter tail and on average two fewer subcaudals. Two of the three Territory specimens, including the type of *H. pulchella*, have the prefrontals longitudinally divided.

Material.—**Western Australia.** *Eastern Division:* SAM R 5295 (Giles, Rawlinson Range); R 17856, R 22019, R 22068, R 22083 (Warburton Range; SAM R 2935 (type of *V. fasciata*). **Northern Territory:** NTM 73 (Alice Springs); NTM 3070 (Nummery, 110 mi. E of Alice Springs); NM D 11226 (type of *H. pulchella*). **South Australia:** SAM R 4801 (Musgrave Park HS.); SAM R 7588 (5 mi. N of Mt. Caroline, Musgrave Park).

Vermicella semifasciata semifasciata

(Günther)

Brachyurophis semifasciata Günther, 1863 : 21. "Baranquilla (New Granada)" [in error for Perth, Western Australia].

Pseudoelaps rhinostomus Jan & Sordelli, 1873 : 6. Southwest Australia.

Diagnosis.—The species *V. semifasciata* is distinguished from other 17-scaled *Vermicella* by nasal contacting preocular, and from other 15-scaled species by prolonged, upturned snout with cutting edge. Present race distinguished from other banded races by 5 upper labials, entire nasal, frequent fusion of primary with secondary temporal, and bands a little narrower to moderately wider than interspaces.

Distribution.—The southwest of Western Australia from Hutt River, Canna and Paynes Find south to Safety Bay, Wickiepin and Kulin; and in eastern interior at Kathleen Valley (north of which it intergrades with *V. s. approximans*), Cosmo Newbery and Warburton Range; thence east into extreme northwestern South Australia.

Description.—Snout very prominent, lower surface of rostral deflected 30-40° up from horizontal. Total length: males 115-302, females 129-353. Tail (% total length): males 8.6-11.2, females 6.0-8.0.

Rostral as high as wide; apex much sharper than right-angle, penetrating deeply between internasals, and reaching back ½-¾ way to frontal (less in juveniles). Internasals about as large as prefrontals. Suture between internasals 0-2.5 times as long as suture between prefrontals. Suture between internasal and prefrontal oblique. Frontal 0.9-1.4 times as long as wide, 0.8-1.1 as long as parietals, and 2.0-3.6 as wide as supraoculars. Nasal entire, almost always contacting preocular which is widely separated

from frontal. Postoculars 2. Temporals basically 1 + 1 + 2, but most specimens have primary and secondary fused; rarer aberrations include fusion of tertiaries and of upper tertiary with secondary. Upper labials normally 5; two specimens have 4 through fusion of first partly with second and partly with rostral; one has 6 through division of last; and one has 7 through division of second and fourth.

Scale rows 17, increasing on neck to 19-21, reducing to 15 immediately before vent in half of specimens. Ventrals: males 147-172, females 155-188. Subcaudals: males 20-26, females 14-20.

Snout with or without dusky markings. Head blotch dark brown, usually beginning a little behind anterior edge of frontal, finishing at end of parietals or a little before, and extending broadly down to level of eyes and sometimes narrowly to lips. Nuchal blotch dark brown, 4-10 scales long, either continuous on midline with head blotch or separated by up to 3 vertebral scales. Back crossed by 40-70 bands, 1-3 scales wide at midbody and separated by interspaces of 1-2½ scales. Tail with 6-10 bands in males, 5-8 in females.

Geographic variation.—Although the apparently isolated northeastern population differs in several characters from west-coast snakes, nearly every gap is bridged by the Wheat Belt series, which in general is only a little more like the coastal snakes than the much more distant northeastern series. Apart from local irregularities, especially in the Darling Range, variation is clinal. Of the seven southwest-northeast clines set out below, those marked with an asterisk extend to the next race, *approximans*.

- (1) increasing size*
- (2) decreasing relative length of tail
- (3) increasing number of ventrals*
- (4) increasing number of subcaudals*
- (5) increasing number of body bands
- (6) increasing width of bands*
- (7) decreasing width of pale interspaces*.

Material.—**Western Australia.** *North-West Division:* R 9157 (Paynes Find). *South-West Division:* R 26849 (Hutt River); R 4509-10 (East Chapman); R 25609 (13 mi. E of Canna); R 2311 (Gutha); R 19883 (Maya); R 2083 (Watheroo); R 6716, R 6955 (Dalwallinu); R 6107 (East Dalwallinu); R 21284 (Mollerin); R 4974, R 8077 (Moora); R 22366 (8 mi. E of Gillingarra); R 26484 (7 mi. N of New Norcia); R 6457 (Koorda); R 5731-2 (Mukinbudin); R 8998 (Bolgart); R 10672 (Dowerin); R 4229 (Wyalkatchem); R 25594 (9 mi. S of Trayning); R 7843 (Mangowine, near Nungarin); R 8582 (Merredin); R 634 (Baandee); R 10557 (York); R 1171 (Narembreen); R 10256 (Kulin); R 7918 (Malyalling); R 22997-8 (North Bindoon); 16 specimens from Darling Range (from Red Hill and Woorooloo south to Kalamunda); R 15825 (6 mi. SE of Yanchep); R 21600 (Wanneroo); R 5915 (Upper Swan); 27 specimens from Perth and suburbs (from Scarborough, Morley and Midland Junction south to Subiaco, Como and Maddington); R 9474 (Gosnells); R 6096, R 6911 (Peel Estate); R 13543 (Safety Bay). *Eastern Division:* R 16524 (20 mi. E of Warburton Mission); R 14660, R 15160, R 22017-8, R 22067, R 22075-9, R 22188-9 (Warburton Mission); R 13854, R 15102-3 (Cosmo Newbery); R 24917 (Kathleen Valley); R 21649 (40 mi. E of Southern Cross); R 5686 (Yellowdine); R

2262 (Marvel Loch); R 5208 (South Walgoolan). **South Australia:** SAM R 5358 (Mt. Davies, Tomkinson Range).

Vermicella semifasciata approximans (Glauert)

Rhynchoelaps approximans Glauert, 1954: 85.
Muccan, Western Australia (D. W. H. Shilling).

Diagnosis.—Distinguished from other races of *V. semifasciata* by weaker snout, less oblique internasal-prefrontal suture, and extremely broad bands separated by extremely narrow interspaces. Further distinguished from *V. s. semifasciata* by 6 (rather than 5) upper labials.

Distribution.—Western arid zone of Western Australia from the De Grey River south and east to Lake Nabberu (south of which it intergrades with nominate race).

Description.—Snout not so prominent as in other races; lower surface of rostral deflected 20-40° up from horizontal. Total length: males 122-362, female 122. Tail (% total length): males 8.9-10.0, female 7.0.

Rostral wider than high; apex rectangular or slightly obtuse, penetrating moderately between internasals, and reaching back 0.4-0.5 way to frontal. Internasals considerably smaller than prefrontals. Suture between internasals 0.3-1.5 times as long as suture between prefrontals. Suture between internasal and prefrontal transverse or slightly oblique. Frontal 1.1 times as long as wide, 0.8-0.95 as long as parietals, and 2.2-4.0 as wide as supraoculars. Nasal entire or weakly grooved (from nostril to labial), contacting preocular which is separated from frontal. Postoculars 2. Temporals 1 + 1 + 2. Upper labials 6.

Scale rows 17, increasing on neck to 19, reducing immediately before vent in one specimen (to 16). Ventrals: males 169-181, female 176. Subcaudals: males 24-28, female 21.

Head blotch extending from about middle of prefrontals nearly to end of parietals and down on sides to level of eye. Nuchal blotch 5-8 scales long, either continuous on midline with head blotch or separated by up to 1½ vertebral scales. Back crossed by 45-68 dark bands, 2½-3½ scales wide at midbody and separated by pale interspaces ½-¾ scale wide. Males with 8-14 bands on tail. Dark markings fading in alcohol to dark, slightly reddish brown, and spaces between bands to brownish white.

Geographic variation.—The specimen from Wiluna agrees in coloration and number of labials with *approximans* (which at Windich Spring occurs only 80 miles to NNE). In rostral development and obliquity of internasals it is more like nominate *semifasciata* (which at Kathleen Valley occurs only 60 miles to south).

Remarks.—Probably owing to faulty redescription (Glauert 1957: 43), *approximans* has been wrongly associated with *V. fasciolata*. That it is nothing more than a race of *V. semifasciata* is demonstrated by the intermediacy of the Wiluna specimen and the fact that *approximans* constitutes the extreme expression of five out of the seven clines observed in nominate *semifasciata*. Moreover, *approximans* is not very different from *V. s. roperi*, which likewise has 6 upper labials, unfused temporals and a tendency for bands to be much wider than pale interspaces.

The coordinates of the type-locality are 20° 38' S, 120° 03' E, not as given by Glauert.

Material.—**Western Australia.** *North-West Division*: R 5375 (De Grey, 37 mi. ENE of Port Hedland); SAM R 3469 (Pilgangoora, 55 mi. SSE of Port Hedland); R 10768 (Muccan, 42 mi. NNE of Marble Bar); NM R 725 (Marble Bar). *Eastern Division*: R 26848 (Windich Spring, Canning Stock Route, north of Lake Nabberu); R 6324 (Wiluna).

***Vermicella semifasciata roperi* (Kinghorn)**

Rhynchoelaps roperi Kinghorn, 1931 : 267. Roper River, Northern Territory (K. Langford Smith).

Rhynchoelaps smithii Kinghorn, 1931 : 267, in caption for Fig. 1 (of *Rhynchoelaps roperi*).

Diagnosis.—Distinguished from *V. s. approximans* by its larger, sharper and more strongly upturned snout and narrower bands separated by wider interspaces.

Distribution.—Kimberley Division of Western Australia and Northern Territory from Roper River south to Hatches Creek.

Description.—Snout very prominent; lower surface of rostral sloping 30–50° up from horizontal; tipped with sharp vertical flange; sides tending to slope up to a midrostral keel. Total length: males 142–350, females 132–368. Tail (% total length): males 8.2–10.7, females 5.5–8.5.

Rostral about as high as wide; apex much sharper than right-angle, penetrating deeply between internasals, and reaching back 0.4–0.7 way to frontal. Suture between internasals 0.5–2.5 times as long as suture between prefrontals. Suture between internasal and prefrontal moderately to sharply oblique. Frontal 1.0–1.3 times as long as wide, 0.8–1.2 as long as parietals, and 2.1–3.5 as wide as supraoculars. Nasal semi-divided (by suture descending from nostril). Preocular contacting nasal but separated from frontal. Postoculars normally 2. Temporals normally 1 + 1 + 2; primary and secondary fused in R 20349; tertiaries fused in R 17127; and secondary longitudinally divided in R 21506. Upper labials normally 6 (5 in R 21500 and on one side of type).

Scale rows 15 or 17, usually increasing by 2 on neck, seldom reducing before vent. Ventrals: males 150–171, females 158–179. Subcaudals: males 20–24, females 15–20. Head blotch beginning either on rostral, internasals, prefrontals or just behind anterior edge of frontals and extending back to about end of parietals and on sides to at least level of eye and often narrowly to lip. Nuchal blotch 3½–9 scales long, either continuous on midline with head blotch or separated by up to 3½ vertebral scales. Back crossed by 34–63 bands, 1¼–3 scales wide at mid-body and separated by interspaces of ½–1¼ scales (at narrowest extreme, interspaces may be merely transverse rows of pale spots). Tail with 5–11 bands in males, 4–8 in females. All dark markings fading in alcohol to reddish or olive brown.

Geographic variation.—The material comes from three regions: Roper River, Kimberley and Tennant Creek. Taken in that order, and ignoring differences in longitude, we find the following north-south trends:

- (1) decreasing relative length of tail,
- (2) increasing number of ventrals,
- (3) increasing number of scale rows (invari-

ably 15 at Roper River, usually 17 in Kimberley, invariably 17 at Tennant Creek),

(4) increasing number of body bands,

(5) decreasing space between bands,

(6) decreasing space between head and nuchal blotches,

(7) frontal becoming shorter and wider.

Other regional variations are non-clinal, e.g. the low subcaudal counts at Tennant Creek (about 2 less than elsewhere), and the smaller and less upturned rostral at Roper River.

Remarks.—From a purely morphological viewpoint, *roperi* is scarcely worthy of separation from the nominate race. The specimen from Tennant Creek with 5 upper labials would probably pass unnoticed in a batch of *V. s. semifasciata*.

From an evolutionary viewpoint, there is more justification for recognising *roperi*. Whereas five of the seven clines observed in the nominate race extend to the superficially very different *V. s. approximans*, few if any extend to the superficially similar *V. s. roperi*. Moreover, the direction of clines 2, 3, 5 and 7 in *s. semifasciata* are reversed in *s. roperi*. A curious effect of these reversals is that relative tail-length, number of ventrals and subcaudals etc. at Roper River are nearer to those at Perth than in any intermediate region.

The occurrence of *V. s. roperi* at Charlotte Waters in the extreme south of the Northern Territory requires confirmation, for in the country to its immediate north only *V. s. incincta* has been collected. On the other hand, the Charlotte Waters specimen is very like females of the northeastern population of *V. s. semifasciata* and differs from them only in having 6 upper labials and a semidivided nasal.

Material.—**Western Australia.** *Kimberley Division*: SAM R 7914 (Wyndham); R 11975 (Kimberley Research Station, Ord River); R 17127 (King Leopold Range); R 13823, R 14187, R 20349 (Derby); R 13822 (4 mi. E of Derby); R 26701-2 (no precise locality). **Northern Territory**: AM R 9930 (holotype); NM D 9834, NM D 10057-8, NM D 10961 (Roper River Mission); R 21505 (Peko, 5 mi. E of Tennant Creek); R 21506-9 (Tennant Creek district); SAM R 2278 (Tennant Creek); SAM R 3634 (Hatches Creek); NM R 11329 ("Charlotte Waters").

***Vermicella semifasciata incincta* subsp. nov.**

Holotype.—R 26844 in Western Australian Museum, an adult male collected on October 16, 1964, by K. R. Slater near Alice Springs, Northern Territory, in 23° 46' S, 133° 53' E. Formerly NTM 2301 in the collection of the Animal Industry Branch, Northern Territory Administration, Alice Springs.

Diagnosis.—Distinguished from all other races of *V. semifasciata* by absence of dark bands on body and tail.

Distribution.—Southern interior of Northern Territory from Mt. Denison south and east to Alice Springs.

Description.—Snout greatly prolonged past mouth; lower surface of rostral deflected 15–35° up from horizontal; tipped with sharp cutting edge. Total length: males 261–292, female 145. Tail (% total length): males 9.1–11.1, female 8.0.

TABLE 1

Mean total length (mm.), tail length (% total length), and number of ventrals and subcaudals in males (with female data in brackets).

	sample size	length	tail	ventrals	subcaudals
<i>annulata snelli</i> (1)	2 (3)	365 (435)	4.8 (4.2)	284 (305)	23.0 (20.7)
" " (2)	3 (2)	374 (348)	5.4 (4.6)	267 (270)	22.3 (18.5)
<i>annulata multifasciata</i>	5 (3)	389 (366)	5.6 (4.5)	259 (277)	21.8 (18.7)
<i>bertholdi bertholdi</i> (3)	21 (15)	183 (185)	11.6 (8.8)	116 (121)	21.7 (17.3)
" " (4)	26 (28)	174 (185)	11.7 (8.7)	116 (123)	22.2 (17.4)
" " (5)	16 (16)	201 (235)	12.3 (9.0)	123 (129)	23.7 (17.9)
<i>bertholdi littoralis</i> (6)	5 (6)	151 (223)	12.0 (9.1)	113 (120)	22.6 (17.8)
" " (7)	3 (4)	171 (252)	13.1 (9.0)	108 (119)	21.0 (17.7)
<i>bertholdi anomala</i>	4 (6)	193 (178)	12.8 (9.6)	125 (126)	25.6 (19.0)
<i>calonotos</i>	23 (32)	227 (239)	14.2 (11.4)	133 (140)	30.6 (26.0)
<i>bimaculata</i> (3)	16 (15)	251 (315)	9.4 (6.8)	185 (205)	27.9 (21.1)
" (5)	4 (4)	281 (375)	8.4 (5.9)	206 (223)	27.5 (20.0)
<i>fasciolata fasciolata</i>	14 (7)	271 (285)	11.8 (8.3)	148 (163)	26.6 (20.6)
<i>fasciolata fasciata</i>	6 (4)	268 (299)	13.5 (8.4)	152 (164)	26.3 (19.4)
<i>semifasciata semifasciata</i> (3)	16 (15)	219 (244)	10.1 (7.3)	156 (165)	22.6 (17.5)
" " (8)	9 (8)	231 (230)	10.0 (6.9)	156 (168)	22.7 (16.7)
" " (4)	12 (18)	217 (265)	10.0 (7.0)	163 (170)	23.4 (17.4)
" " (9)	5 (13)	251 (285)	9.5 (6.8)	166 (178)	24.0 (18.0)
<i>semifasciata approximans</i>	6 (1)	249 (122)	9.5 (7.0)	175 (176)	25.8 (21.0)
<i>semifasciata roperi</i> (10)	5 (2)	246 (266)	8.9 (5.9)	165 (178)	20.4 (15.5)
" " (11)	6 (2)	274 (306)	9.7 (7.3)	156 (168)	22.5 (18.0)
" " (12)	1 (4)	281 (243)	10.1 (8.1)	150 (161)	22.0 (18.3)
<i>semifasciata incincta</i>	3 (1)	236 (122)	10.1 (8.0)	153 (157)	22.7 (20.0)

(1) Pilbara, (2) Northern Territory, (3) Swan Coastal Plain, (4) Wheat Belt, (5) north and east, (6) south, (7) north, (8) Darling Range, (9) northeast, (10) Tennant Creek, (11) Kimberley, (12) Roper River.

Rostral about as high as wide; apex considerably sharper than right-angle penetrating deeply between internasals (completely separating them in NTM 2262), and reaching back 0.55-0.6 way to frontal. Suture between internasals (when present) 0.5-1.1 times as long as suture between prefrontals. Suture between internasal and prefrontal oblique. Prefrontals longitudinally divided in NTM 2262. Frontal 0.9-1.2 times as long as wide, 0.8-1.0 as long as parietals, and 2.2-3.0 as wide as supraoculars. Nasal entire or grooved (from nostril down to labial), contacting preocular which is separated from frontal. Postoculars 2. Temporals basically 1 + 1 + 2; no fusion, but primary divided in NTM 2263. Upper labials 6.

Scale rows 17, increasing on neck to 19; no reduction before vent. Ventrals: males 146-161, female 157. Subcaudals: males 22-24, female 20.

Head blotch blackish brown, beginning just in front of eyes and extending back nearly to end of parietals and on to side of head but not to lip; anterior margin arched back on midline. Nuchal blotch blackish brown, $4\frac{1}{2}$ -5 scales long, separated from head blotch by 4-5 vertebral scales. Upper surface of rostral greyish brown. Back and tail unbanded; scales pale, narrowly margined darker.

Geographic variation.—The Mt. Denison snakes differ from the Alice Springs snakes as follows:—

- (1) dorsal and supracaudal scales pale reddish brown, edged with dark reddish brown (at Alice Springs the scales are whitish or pale grey and edged with blackish brown),
- (2) relatively shorter tail,
- (3) more ventrals,
- (4) fewer subcaudals.

Remarks.—In certain respects *incincta* is more like the eastern race, *V. s. australis* (Krefft), than any of the western races of *V. semifasciata*. It shares with *australis* low number of ventrals and wide separation of head and nuchal

blotches; and its complete lack of bands is foreshadowed by their extreme narrowness in *australis*.

Mr. K. R. Slater kindly donated the holotype to the Western Australian Museum.

Paratypes.—**Northern Territory:** NTM 2262-3 (Mt. Denison, 160 mi. NW of Alice Springs); NTM 63 (Alice Springs).

Discussion

Three things point to *Vermicella* being an old and declining genus: its lack of young species, the concentration of species in the southwest of the continent, and the disappearance of links with other genera.

By a young species I mean one which has so recently attained species status that it is still possible to say where it evolved and from what. A typical situation is where two closely related forms are mainly allopatric but have a small zone of overlap. There is nothing like this in *Vermicella*: sympatries are generally broad, and no two species are so close that one could postulate the characters of their common ancestor. Some species, like *bertholdi*, have had time to evolve very distinctive subspecies; others, like *calonotos*, to judge from their shrinking range, must be on the verge of extinction.

Five of the seven species occur in the vicinity of Perth, a locality notable for such reptilian relicts as *Pseudemydura* and *Pletholax*. In contrast, over most of northern and eastern Australia there are only two species, *annulata* and *semifasciata*. These species, it will be noticed, constitute the adaptive extremes of the genus.

It seems, then, that *Vermicella* has had to break new ground to survive in a region that is open to invasion by modern reptiles from the north.

Even though our knowledge of the comparative anatomy of Australo-Papuan Elapidae is very sketchy, I think one can safely say that *Vermicella* has no close relatives among living snakes. Not knowing whether *Vermicella* is derived from a fossorial stock or from more

TABLE 2

Mean width (in vertebral scales) of occipital bar, nuchal blotch and midbody bands and interspaces, and mean number of bands (dorsal + caudal).

	width of				number of bands
	occipital bar	nuchal blotch	bands	interspaces	
annulata snelli (1)	1.1	7.0	4.7	1.9	52
" " (2)	1.6	8.0	5.0	2.5	39
annulata multifasciata	0.8	7.6	3.3	1.1	67
bertholdi bertholdi (3)	1.3	6.0	2.4	2.9	24
" " (4)	1.4	6.4	2.6	2.7	23
" " (5)	1.7	6.1	2.5	2.8	26
bertholdi littoralis (6)	1.7	3.0	1.7	2.3	37
" " (7)	1.6	3.8	2.2	2.8	24
bertholdi anomala	1.9	5.8	1.8	2.7	31*
calonotos	2.5	3.7
bimaculata (3)	3.3	4.8
" " (5)	3.2	4.2
fasciolata fasciolata	0.7	9.8	0.8	1.3	76
fasciolata fasciata	1.7	4.6	1.6	1.5	70
semifasciata semifasciata (3)	1.6	5.9	1.4	1.6	59
" " (8)	1.1	5.8	1.8	1.5	58
" " (4)	1.9	5.7	1.7	1.6	63
" " (9)	1.5	6.1	2.0	1.5	67
semifasciata approximans	0.9	6.7	2.8	0.6	69
semifasciata roperi (10)	0.6	4.6	1.9	0.9	64
" " (11)	1.3	5.9	2.2	1.3	57
" " (12)	2.3	6.6	2.1	1.5	45
semifasciata incincta	4.5	4.9

* Excluding type of *Melœardina minima*.

(1) Pilbara, (2) Northern Territory, (3) Swan Coastal Plain, (4) Wheat Belt, (5) north and east, (6) south, (7) north, (8) Darling Range, (9) northeast, (10) Tennant Creek, (11) Kimberley, (12) Roper River.

generalised elapids, we are also ignorant as to which of its characters are primitive and which are specialised. We must therefore content ourselves with a brief survey of the extant species.

Table 1 reveals considerable correlation between number of ventrals, total length and (inversely) relative length of tail. Most taxa have an average length of between 20 and 30 cm. In *V. bimaculata* and still more clearly in *V. annulata*, increase in size has been effected by elongation of the trunk. Conversely the small size of *V. bertholdi* has resulted from shortening of the trunk. Now *bertholdi* and *annulata* comprise a group somewhat apart from the other species of *Vermicella*. Consequently the degree of elongation can have no phylogenetic significance in this genus.

Nor does absence of bands provide a clue to phylogeny, for their loss in the race *incincta* of *V. semifasciata* and in the variant "*minima*" of *V. bertholdi anomala* seems to have been recent and sudden events. Moreover, consideration of the sequence *bimaculata-fasciolata-semifasciata* suggests how lost bands could be reacquired. In the unbanded *bimaculata* all the dorsal scales have dark margins which are thickest at their free edges. Single transverse rows of such scales are virtually all that constitute the bands of *V. f. fasciolata*. When the margin is more uniform in width and the adjacent scale-rows become involved, we have the narrow, reticulate bands of *V. fasciolata fasciata* and *V. semifasciata australis*. Increasing encroachment of the dark margins on the pale centres of the scales and increasing involvement of neighbouring scale-rows would lead first to the solid but still narrow bands of Swan River *V. s. semifasciata* and finally to the extremely broad bands of *V. s. approximans*.

Instead of crossbands, *V. calonotos* has a vertebral stripe, but the scales composing the stripe are precisely like those of the taxa with reticulate bands. Evolution of the stripe (incipient in individual variants of *V. bimaculata*)

can be imagined as taking place in two steps. At first the wide-margined scales are confined to those dorsal and caudal segments having a potential for band-formation. Then, by a process not different from what must have occurred in the taxa with broad bands, the margined scales invade the interannular zones till the stripe is continuous.

"Segments having a potential for band-formation" implies that, though bands may be lost, the faculty for forming them in definite sites is retained. This belief is based on (1) the persistence in all taxa of a nuchal blotch, (2) the presence in most taxa of a head blotch, (3) the prevailing constancy among taxa of the position of these blotches, and (4) the evident homology of these blotches with the caudal and dorsal bands.

From the first two columns in Table 2 it will be seen that the nuchal blotch, though varying much in extent, is centred in nearly all taxa on the fourth or fifth vertebral scale. Similarly the head blotch tends to be centred midway between the anterior edge of the frontal and the posterior edge of the parietals (so that whenever the blotch fails to reach back to the end of the parietals, it usually fails also to reach forward to the prefrontals).

That the blotches and bands are serially homologous is indicated by (1) their generally identical coloration within a taxon, (2) the fact that the head and nuchal blotches extend to the lower surface only in the taxa whose bands do likewise, (3) the presence in the nuchal blotch of some individuals of *V. calonotos* of white-centred scales like those of the vertebral stripe, and (4) the similarity in many taxa between the nuchal blotch and the anteriormost dorsal bands with respect to extent and interspacing.

The sequence *bimaculata-fasciolata-semifasciata* is also one of increasing rostral development. The snout is produced well past the mouth in *bimaculata* but lacks a cutting-edge. In *fasciolata* we see the beginnings of the cut-

TABLE 3

Mean ratio between (1) length of rostral and distance from tip of snout to frontal, (2) length of suture between internasals and that between prefrontals, (3) length of frontal and its width, (4) width of frontal and width of supraocular, and (5) length of parietal and length of frontal.

	rostral	internasal	frontal length	frontal width	parietal
<i>annulata snelli</i>	0.38	0.6	1.7	1.7	1.4
<i>annulata multifasciata</i>	0.34	1.7	1.9	1.4
<i>bertholdi bertholdi</i>	0.34	1.0	2.0	1.8	1.4
<i>bertholdi littoralis</i>	0.36	1.1	1.7	1.9	1.7
<i>bertholdi anomala</i>	0.38	1.2	1.7	2.2	1.3
<i>calonotos</i>	0.35	0.8	1.3	3.0	1.3
<i>bimaculata</i>	0.60	1.0	1.2	2.9	1.4
<i>fasciolata fasciolata</i>	0.41	1.4	1.5	2.5	1.1
<i>fasciolata fasciata</i>	0.34	1.0	1.5	2.3	1.1
<i>semifasciata semifasciata</i>	0.58	0.7	1.2	2.8	1.1
<i>semifasciata approximans</i>	0.47	0.9	1.1	2.7	1.1
<i>semifasciata roperi</i>	0.53	1.0	1.1	2.7	1.0
<i>semifasciata incincta</i>	0.56	0.6	1.1	2.5	1.1

ting-edge which is such a prominent feature of *semifasciata*. Associated with this trend are those of increasing obliquity of the anterior head-shields (internasals and prefrontals) and of increased shortening and widening of the posterior shields (frontal and parietals).

Fusion of head scales is common in *Vermicella*; but the precise nature of the fusions, like the details of habitus, coloration and rostral development, throws little light on the phylogeny of the species. The nominate race of *V. semifasciata* shares with *V. bimaculata* high frequency of fusion between the last two labials and between the primary and secondary temporals; yet in other western races of *semifasciata* both of these fusions are rare. In the nominate race of *V. fasciolata* fusion is moderately common between the tertiary temporals, and the lower postocular is often fused to a neighbouring scale; such fusions, however, are unknown in the northeastern race, *fasciata*, but recur in several other species. Fusion of internasals with prefrontals is diagnostic of *V. annulata multifasciata*; in *V. calonotos* it is a rare aberration. Though all these modes of fusion (and the much rarer fissions) are too irregularly distributed to reveal relationships, the very fact that they are limited in kind and may crop up anywhere in the genus reinforces the belief that this assemblage of species is a natural one.

Finally we may recapitulate the principal trends in *Vermicella*. First we have the annulate spaces, *bertholdi* and *annulata*, which are further characterised by a deep primary temporal and relatively long and narrow frontal and parietals. *V. bertholdi* has become adapted for burrowing in sand; its body is short and its snout flat and sharp in profile (like that of its scincid analogue, *Rhodona*). *V. annulata* has become adapted for an active, nocturnal way of life; its body is elongate, the snout rounded in profile and relatively high, and all lipochromes have been lost (in contrast to *bertholdi* whose only white interannular zone is that between the head and nuchal blotches).

The other sequence of species, *calonotos* to *semifasciata*, is non-annulate or even unbanded. Their frontal is relatively short and wide, the anterior temporal long and low, and the last labial very much larger than the others. Fusion is common between temporals. The parietals are generally short and the rostral strongly developed. Only one of the species, *semifasciata*, is widespread, and it is this species that is most

specialised for burrowing in heavy soils. The other species are fossorial in a more generalised way and are probably yielding ground to the lygosomatine skinks.

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11.—The development of the gametophyte and young sporophyte of *Ecklonia radiata* (C.Ag.) J.Ag. (Laminariales)

by R. Jennings*

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Abstract

Gametophytes and young sporophytes of *Ecklonia radiata* have been grown under controlled environmental conditions, and their structure and development is described. Both the male and female gametophytes are very reduced compared with those of most other members of the order. A periodic alternation of cell division and elongation was observed during the development of male gametophytes.

Introduction

Ecklonia radiata (C.Ag.) J.Ag. is the only representative of the Laminariales found in Western Australian waters. It occurs throughout the waters of southern Australia, Lord Howe Island and New Zealand (Lindauer *et al.*, 1961). The life history of this plant has not hitherto been studied, and it is the purpose of this paper to record the development of its gametophyte and young sporophyte.

Materials and methods

Mature sporophytes were collected from reefs in the shallow sub-littoral zone at Cottesloe, during the period March to July inclusive. Fertile areas of the thallus were located by examining sections under the microscope. These areas were thoroughly inspected under a dissecting microscope, and only segments which appeared free of epiphytes were used in the following work.

Cultures were prepared in the manner described by Papenfuss (1942). Suitable material was kept out of water for several hours to help promote spore release. Pieces of thallus, about 6 cm square, were then immersed in filtered sea water and brushed with a camelhair brush to remove excess mucilage. They were then placed for several minutes in petri dishes of filtered sea water containing microscope slides. Zoospores were released during this period, and a further 12-24 hours were allowed for them to become attached to the slides. The slides were then removed, and filtered sea water was run over them to wash away as many diatoms and protozoa as possible.

The slides were then placed in 14 cm-diameter petri dishes (5 slides per dish) containing 100 ml of nutrient solution. This consisted of NaNO_3 0.1g; Na_2HPO_4 0.02g; distilled water 50 ml; filtered sea water 1,000 ml (Schreiber, 1930). Five ml. of ethylene diamine tetraacetic acid (E.D.T.A.), 3.7 g/l, was included as a chelating agent. The medium was not changed during the period of growth. The cultures were placed in growth cabinets under a light intensity in the

region of 1500 foot candles provided from a mixture of fluorescent tubes and incandescent globes. The daylength was 16 hours, the temperature 22°C.

Slides were removed and examined from time to time, and returned to the nutrient solution immediately after examination. In order to gain an estimate of variation between individuals, 20 randomly selected plants were examined. Illustrations were drawn from living material, but observations on nuclei were made from plants stained with Harris' Haematoxylin (Johansen 1940).

Observations

The gametophyte

After a period of motility ranging from minutes to several hours, zoospores come to rest on the substratum, assume a rounded form and secrete a wall. Germination begins almost immediately, and in six-hour cultures a number of spores have recognizable germ tubes. There appear to be two main patterns of germination.

Firstly, the end of the germ tube swells, giving the "dumbbell" appearance described in related plants (Papenfuss 1942; Kanda 1941). In some cases the entire protoplast migrates into the swollen portion (Fig. 1a), and a cross wall may or may not form. Alternatively, part of the protoplast may remain in the spore case. If a cross wall does form, the cytoplasm in the spore degenerates, but if not the spore appears to remain living.

Secondly, the germ tube remains tubular (Figs. 1b,c), and a cross wall may or may not form. If no wall is formed, part of the protoplast may remain within the spore case.

By the third day, all plants exist in one of these conditions, after which further vegetative growth occurs over a period of seven days. The subsequent growth can be divided into several distinct phases (Fig. 2). From day 3 to 5 there is a period during which the single-celled plant elongates, and between days 5 and 7 an increase in cell number occurs. Cell extension again predominates between day 7 and 9, following which all further growth is, in the main, attributable to an increase in cell number.

Extension of the plant may occur in the plane containing the spore case and germ tube (Fig. 1a), or at various angles to this (Figs. 1f,g). In the latter case, the first cell may extend in one direction (Fig. 1f) or in opposite directions (Fig. 1g).

Male and female plants may be clearly distinguished after 10 days (Figs. 1f,i). The female plants are invariably more heavily pigmented

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than the males, and the cells of the females are approximately twice the length and breadth of the cells of the males. At maturity male plants are on the average 1.4 times as long as female plants. This difference is due to the fact that each male plant consists of two to five cells, while 90 to 95 per cent of female plants comprise only one cell (Table 1). It seems certain that male and female plants begin to differ in development between days 5 and 7, for at day 7, 50 per cent of plants were found to have undergone a single nuclear and cell division. This division was almost certainly restricted to male plants.

TABLE 1

Length and cell number of eleven-day-old male and female gametophytes of *Ecklonia radiata*. Standard errors are given in brackets.

	Male Gametophyte	Female Gametophyte
Mean length (microns)	34.3 (3.2)	23.7 (2.3)
Mean cell number	3.2 (0.4)	1.1 (0.1)

Reproductive structures begin to differentiate by days 10 to 11, when vegetative growth ceases. In male plants antheridia appear as lateral or terminal projections which are eventually separated from the parent cell by a wall. More than one antheridium may be produced from one cell, and up to nine have been observed on one plant. It is possible that more may form during prolonged culture. The antheridium is almost colourless, and the entire protoplast forms a single spermatozoid, which escapes through a terminal pore (Fig. 1k). The spermatozoids may be pyriform or spherical, and of the order of 5 microns in length or diameter respectively. They are biflagellate, and do not have eye spots.

The single cell of a typical female plant develops into an oogonium, in which the protoplast becomes a single ovum with a densely granular appearance and strong pigmentation. Many plants release ova by day 14 (Fig. 1). During the release a marked internal orienta-

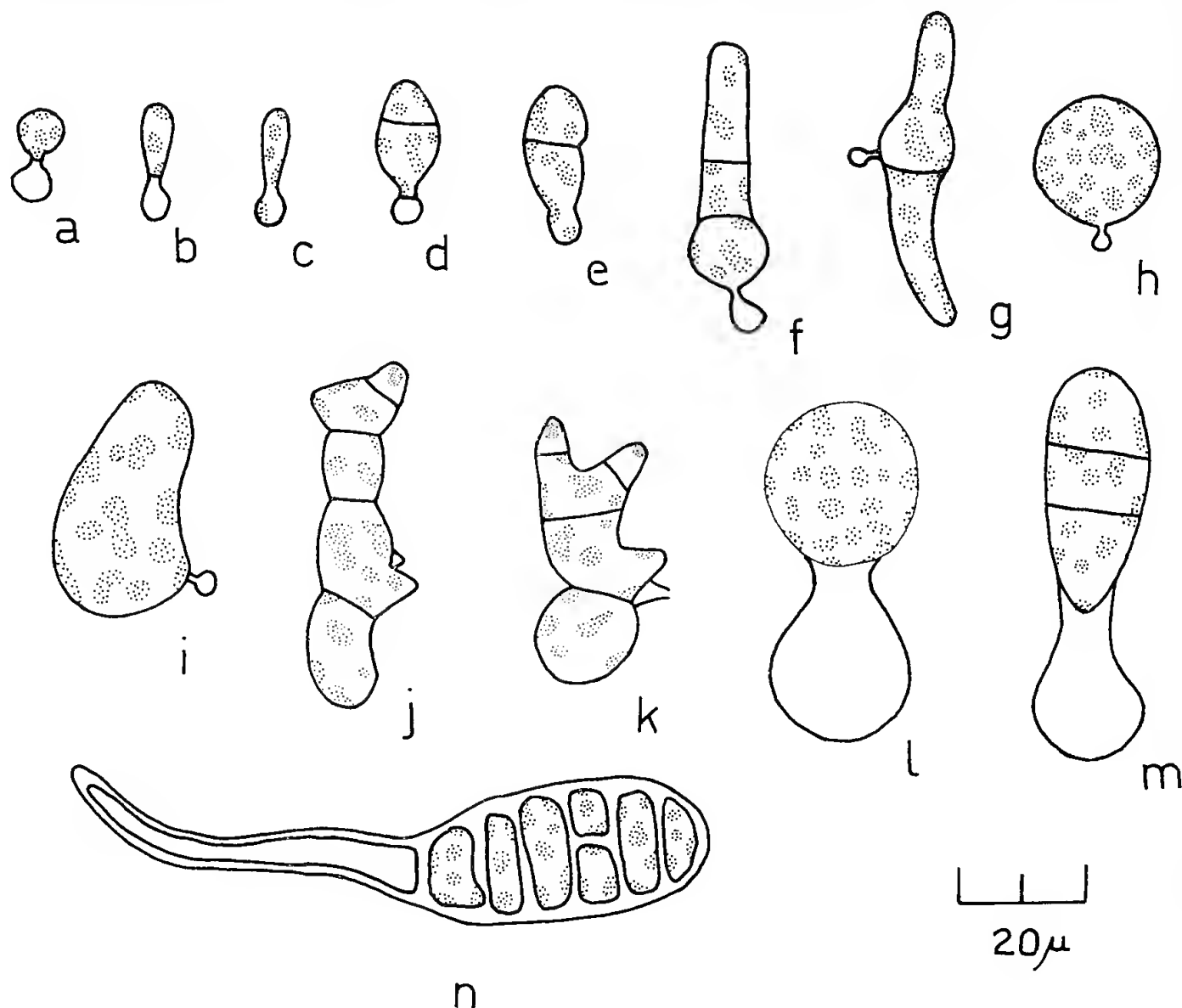


Fig. 1.—Stages in the development of the gametophyte and young sporophyte of *Ecklonia radiata*. All figures are camera lucida drawings of plants grown in nutrient solution. a, b, c, gametophytes, 3 days old. d, e, gametophytes, 6 days old. f, g, male gametophytes, 10 days old. h, i, female gametophytes, 10 days old. j, male gametophyte, 11 days old, showing developing antheridia. k, male gametophyte, 14 days old, one antheridium empty. l, female gametophyte, 14 days old, egg extruded from oogonium. m, young sporophyte. n, young sporophyte, showing rhizoid development.

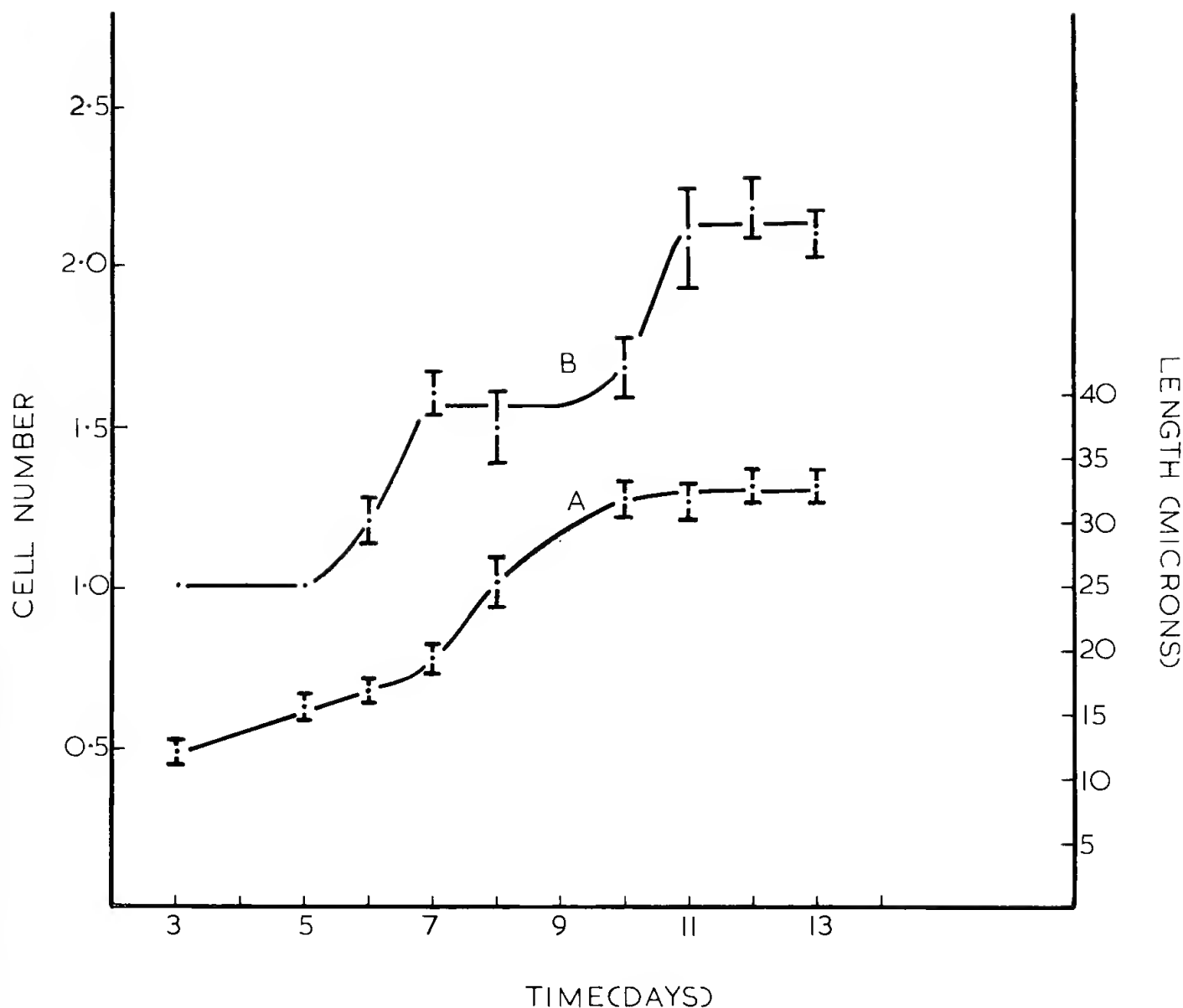


Fig. 2.—Length (A) and cell number (B) of *Ecklonia radiata* gametophytes. Vertical bars indicate standard errors.

tion of cell inclusions is noticeable. Fritsch (1945) suggested that similar phenomena in related plants may be due to strong internal pressures playing a role in dehiscence. The ovum, which is generally spherical but which may occasionally be spheroidal, remains attached to the lip of the oogonial case during fertilization and early development of the sporophyte.

Despite the constant culture conditions, development of gametophytes was found to be much slower in winter than in summer. This has also been observed for *Ecklonia maxima* by Papenfuss (1942). Detailed observations were not made beyond day 10 in winter, when plants were at a similar stage of development as those in 5 day-old summer cultures.

The young sporophyte

Development of the young sporophyte commences soon after fertilization, and while still attached to the oogonial lip. The zygotic cell commences to elongate before transverse divi-

sions occur (Fig. 1m). Between 4 to 10 cells are usually formed in this manner before longitudinal septation begins. All cells, with the exception of the basal cell, undergo longitudinal division. By the time the plant is 4 to 8 cells long, the basal cell has become elongate, and forms the first rhizoid (Fig. 1n). The chromatophores degenerate rapidly. This situation was observed in a number of 12 to 15 day-old plants. Development was not followed beyond this stage.

Discussion

The development of *Ecklonia radiata* gametophytes and young sporophytes is in general similar to that described for other members of the genus *Ecklonia* (Papenfuss 1942; Kanda 1941), and the order Laminariales (Fritsch 1945), but there are differences in detail. It would seem that in most other species of the order, germination of the zoospores involves either the migration of all of the protoplasm from the spore, or the degeneration of any remaining in the spore. An exception is *Alaria*

esculenta, where the spores have been reported by Sauvageau (1916) to retain some cytoplasm and to germinate again to form a second gametophyte. In contrast, in *Ecklonia radiata* cytoplasm may remain in the spore, which continues as a living part of the plant.

Both male and female plants are extremely reduced, with most female plants having no vegetative filaments. This is a condition recorded for *Ecklonia cava* and *Ecklonia stolonifera* (Kanda 1941), though not for *Ecklonia maxima* (Papenfuss 1942). Unicellular female plants and reduced male plants are also reported in several other laminarian genera (Fritsch 1945; Evans 1965). The form and size of gametophytes have been shown to be affected to some extent by temperature, light intensity and nutrient solution (Fritsch 1945; Kanda 1941; Evans 1965), and so the possibility remains that less reduced gametophytes could develop under cultural conditions other than those used here.

Correlated with the reduced nature of the gametophytes is the unusually early stage at which the sexes begin to differ in development, and the early formation of reproductive organs. Kanda (1941) reports a similar situation to exist with *Ecklonia cava* and *Ecklonia stolonifera*, while Williams (1921) and Evans (1965) have made similar observations for *Laminaria* species. Gametophytes of most other Laminariales are considerably larger, and both the visible distinction of the sexes and the development of reproductive organs occurs much later in development; for example, this is the case with *Ecklonia maxima* (Papenfuss 1942).

Evans (1965) suggested the possibility that there is a rhythm of cell divisions during gametophyte growth. This is clearly the case with *Ecklonia radiata*, and similar methods of analy-

sis may prove it to be widespread among laminarian gametophytes. It would be of interest to study the periodicity of the divisions in relation to variation in the environmental conditions.

Kanda (1941) has reported that the basal cell of the young sporophyte of *Ecklonia cava* elongates, but is not involved in rhizoid formation. In this respect it is clear that *Ecklonia radiata* more closely resembles *Ecklonia maxima*, for Papenfuss (1942) found that its basal cell becomes rhizoidal.

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12.—Additions to the flora of Western Australia: ten miscellaneous
new species

by A. S. George*

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Abstract

The following new species are described: *Grevillea calcicola* (Proteaceae), *Stachystemon axillaris* (Euphorbiaceae), *Pomaderris bilocularis* (Rhamnaceae), *Guichenotia apetala* (Sterculiaceae), *Darwinia repens* (Myrtaceae), *Xanthosia tomentosa* (Apiaceae), *Styphelia intertexta* (Epacridaceae), *Ipomoea yardiensis* (Convolvulaceae), *Pityrodia canaliculata* and *Pityrodia scabra* (Dieracrydiaceae).

PROTEACEAE

Grevillea calcicola sp. nov. Sect. *Lissostylis*.

Frutex ad 4m altus, caulis pluribus ramosissimis. Ramuli foliaque juvenes pubescentes, mox glabri. Folia pinnatisecta, 7-20 cm longa, lobis usque ad 7, linearibus, marginibus revolutis. Flores albi in racemis paniculatis terminalibus; rachis pedicellique glabri. Bractee lanceolatae, concavae, paulum hirsutae, 0.75 mm longae, deciduae. Pedicelli 3-4 mm longi. Perianthium 3.5-4 mm longum, angustum, sub limbo revolutum, glabrum praeter pilos paucos in tubo. Stylus glaber 9 mm longus, disco ovato laterale. Ovarium longe stipitatum; torus rectus, glandula hypogyna laterale prominente. Fructus stipitatus, oblongo-ovoideus, compressus. 2.5 cm longus, 1 cm latus. Semina elliptica alis latis annulatis.

Holotype: Charles Knife Road, Cape Range, A. S. George 1331, Aug. 30, 1961.

Shrub to 4 m with several much-branched stems. Branchlets and young leaves pubescent, becoming glabrous. Leaves pinnatisect, 7-20 cm long, lobes up to 7, linear, closely revolute. Flowers white in racemes forming a terminal panicle. Rachis and pedicels glabrous. Bracts lanceolate, concave, hirsute on the margins and towards the apex, about 0.75 mm long, deciduous. Pedicels 3-4 mm long. Perianth 3.5-4 mm long, narrow, revolute under the limb, glabrous except for a few scattered hairs inside. Style glabrous, about 9 mm long; stigmatic disc ovate, lateral. Ovary on a long stipe; torus straight, with a prominent, lateral hypogynous gland. Fruit stipitate, oblong-ovoid, compressed, 2.5 cm long, 1 cm broad. Seeds elliptical, with broad, annular wings.

The species is closest to *G. berryana* Ewart et White (which is in the Section *Lissostylis*, not *Cycloptera*, as stated in the original description), differing in the rachis and pedicels being glabrous, the flowers almost so, and in the larger, oblong-ovoid fruit.

It is known only from the Cape Range below North-West Cape, where it always occurs in limestone soil (hence the specific epithet). The holotype is in flower only, but fruiting material has been collected by Y. Chadwick, 1393, 5 miles S. of Yardie Creek homestead.

EUPHORBIACEAE (PORANTHEROIDEAE)

Stachystemon axillaris sp. nov.

Frutex erectus, tenuis, glaber, ad 70 cm altus. Folia 0.5-3 cm longa, plerumque 1.5-2.5 cm, late-linear, obtusa vel acutiuscula, breviter petiolata; stipulae scariosae, lanceolatae, acutae, decurrentes. Flores virides, axillares, solitarii vel plures, ♂ supra ♀ sed saepe 1 ♀ cum 2 ♂, bracteis paucis parvis scariosis. Flores ♂ pedicellati, ± 1.75 mm diam.; segmenta perianthii herbacea, inaequalia, triangularia vel angustelanceolata, obtusa, incurva; stamina numerosa filamentis brevibus inaequalibus in receptaculo convexo. Flores ♀ breviter pedicellati; segmenta perianthii 2.5-3 mm longa, scariosa, lanceolata, acuta, integra vel irregulariter serrata; ramuli styli 2 raro 3, recurvi. Capsula ovoidea, compressa, 5-6 mm longa (sine styli ramulis persistentibus), abortu monosperma; placenta ab septo secedens. Semen oblique oblongum 4-5 mm longum, carunculatum, hilo impresso.

Holotype: 5 miles W of Mogumber Siding, A.S. George 6828, Sept., 17, 1965.

An erect, slender, glabrous shrub to 70 cm. Leaves 0.5-3 cm long, usually 1.5-2.5 cm, broadly linear, obtuse or somewhat acute, shortly petiolate; stipules scarious, lanceolate, acute, decurrent. Flowers green, axillary, solitary or several, the ♂ above the ♀ but often 1 ♀ between 2 ♂, with a few small scarious bracts. Male flowers pedicellate, about 1.75 mm diam.; perianth segments herbaceous, unequal, triangular to narrow-lanceolate, obtuse, incurved; stamens numerous with short unequal filaments on a convex receptacle. Female flowers shortly pedicellate; perianth segments 2.5-3 mm long, scarious, lanceolate, acute, entire or irregularly serrate; style branches 2, rarely 3, recurved. Capsule ovoid, compressed, 5-6 mm long (without the persistent style branches), one-seeded by abortion; placenta separating from the septum. Seed obliquely oblong, 4-5 mm long carunculate, the hilum impressed.

The species differs from the other three of the genus principally in having the flowers axillary, not crowded at or below the apices of the branchlets so as to appear whorled; and in

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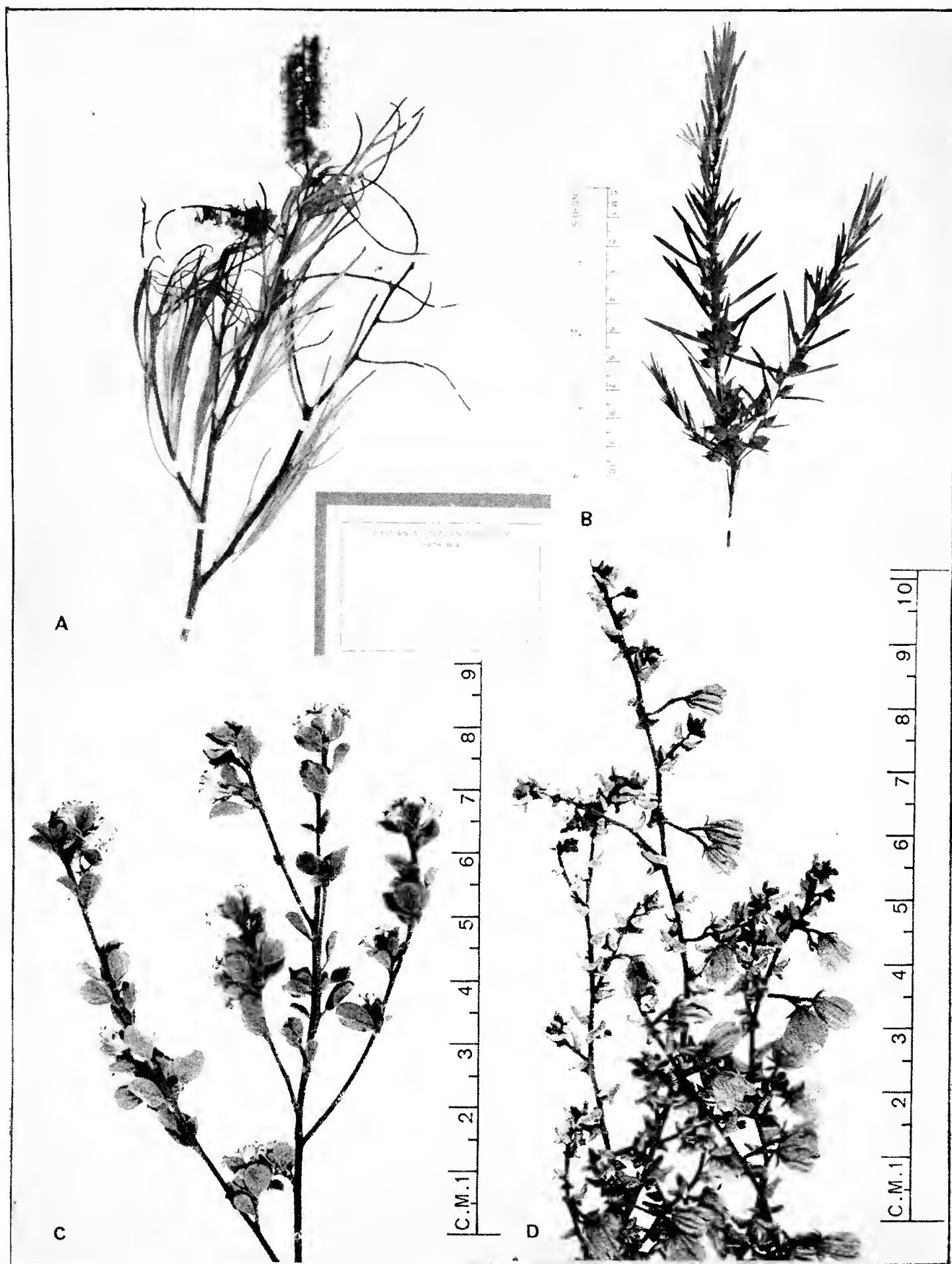


Figure 1.—All photographs from type collections. A. *Grevillea calicola* sp. nov.; B. *Stachystemon axillaris* sp. nov.; C. *Pomaderris bilocularis* sp. nov.; D. *Guichenotia apetala* sp. nov.

the short convex receptacle of the male flowers. There are further differences in the floral morphology. It is also known from Wanneroo (J. Havel 177) and 4 miles S. of Cockleshell Gully (George 7814).

RHAMNACEAE

Pomaderris bilocularis sp. nov.

Frutex gracilis ad 50 cm altus, dense tomentosus pilis stellatis simplicibusque. Folia obovata-cordata, truncata, 4-9 mm longa, petiolis 1-1.5 mm longis. Stipuli lanceolati, acuti, brunnei, scariosi, \pm 2 mm longi, extus tomentosi, intus pilis appressis hirsuti. Flores lutei, terminales, corymbosi. Pedicelli 3-4 mm longi. Lobi calycis lanceolati 1.5-2 mm longi, quam tubum multo longiores, extus tomentosi, intus glabri costa media. Petala nulla. Discus nullus. Stamina exserta. Stylus crassus, parum 2-lobatus. Ovarium semi-inferum, ad summum tomentosum, biloculare loculis uniovulatis. Fructus semi-exserta, dehiscentia septicidale. Semina oblonga, laevia, arillata.

Holotype: Tuttanning Reserve, East Pingelly, A. S. George 7355, Nov. 16, 1965.

A slender shrub to 50 cm, densely tomentose with stellate and simple hairs. Leaves obovate-cordate, truncate, 4-9 mm long including the petiole of 1-1.5 mm. Stipules lanceolate, acute, brown and scarious, \pm 2 mm long, tomentose outside, hirsute with simple appressed hairs within. Flowers yellow, terminal, corymbose. Pedicels 3-4 mm long. Calyx lobes lanceolate, 1.5-2 mm long, much longer than the tube, tomentose outside, glabrous within with midribs. Petals none. Disc none. Stamens exserted. Style thick, slightly 2-lobed. Ovary half-inferior, densely tomentose on top, 2-celled with one ovule per cell. Fruit semi-exserted, with septicidal dehiscence. Seeds oblong, smooth, arillate.

This species differs from the other petal-less species of the genus in the very shortly lobed style and the 2-celled ovary. The fruit is described from George 7744, also from Tuttanning.

STERCULIACEAE

Guichenotia apetala sp. nov.

Frutex ramosissimus ad 35 cm altus. Rami foliaque juvenes dense stellato-tomentosi. Folia 2-5 mm longa, patentia, subsessilia, triangulare-cordata, ad basin subauriculata, obtusa, marginibus revolutis; tomentosa, supra glabrescentia reticulatovenosa. Stipulae nullae. Flores salmonacei, solitarii vel racemosi; pedunculi quam foliis longiores recurvi, tomentosi. Bractaeae bracteolaeque lineares. Calyx campanulatus 5-7 mm longus, lobis obtusis trinervis, extus stellato-tomentosus, intus tubus glaber, lobis pubescentibus. Petala nulla. Stamina libera antheris 1.5 mm longis. Staminodia nulla. Ovarium 3-loculatum, dense tomentosum, loculis 2-ovulatis; stylus 4 mm longus, gracilis, glaber vel ad basin sparsim stellato-tomentosus. Fructus crustaceus, loculis monospermis. Semina fusca, 2 mm longa, oblonga, laevia, strophiolata.

Holotype: Mt. Desmond, SE of Ravensthorpe, T.E.H. Aplin 2693, Oct. 27, 1963.

A much-branched shrub up to 35 cm. Young branches and leaves densely stellate-tomentose. Leaves 2-5 mm long, spreading, subsessile,

triangular-cordate, sub-auriculate, obtuse, the margins revolute; tomentose, becoming glabrous and reticulately-nerved above. Stipules none. Flowers salmon-pink, solitary or shortly racemose; peduncles longer than the leaves, recurved, tomentose. Bracts and bracteoles linear. Calyx campanulate 5-7 mm long, the lobes obtuse, 3-nerved; stellate tomentose outside, glabrous within except for the pubescent lobes. Petals none. Stamens free, anthers 1.5 mm long. Staminodia none. Ovary 3-celled, densely tomentose, with 2 ovules per locule; style 4 mm long, slender, glabrous or sparsely stellate-tomentose at the base. Fruit crustaceous, loculi 1-seeded. Seeds dark brown, smooth, strophiolate, 2 mm long.

This species, lacking stipules and petals, is somewhat anomalous in the genus, but it has the typical ribbed calyx and general habit. It is closest to *G. micrantha* (Steetz) Benth., which occasionally lacks stipules also, differing further in the leaf shape, the glabrous style and the 3-celled ovary. It is known only from the Mt. Desmond area, and has also been collected by K. Newbey (no. 568), F. Humphreys, and A.S. George (1643).

MYRTACEAE (CHAMELAUCIEAE)

Darwinia repens sp. nov.

Frutex glaber ramis prostratis, saepe ad nodos radicanter, etiam ramulis brevibus erectis. Folia opposita, conferta, linearia, teretia-triquetra, 5-10 mm longa, parum scaberula; folia floralia similia. Flores axillares rubri, in pedicellis brevibus crassis. Bracteolae ovatae, scariosae, brunneae, mucronatae, 2.5-3 mm longae. Calycis tubus cylindricus \pm 4 mm longus, lobis orbicularibus breviter ciliatis \pm 1 mm longis. Petala ovali-oblonga 2-3 mm longa. Stamina staminodiaque ad basin breviter connata. Stamina 0.75 mm longa antheris obovatoideis. Stylus gracilis, \pm 15 mm longus; stigma parva, a paucis ciliis subtenta. Ovuli 8.

Holotype: 15 miles E. of Mingenew: A. R. Main.

A prostrate, glabrous shrub, often rooting at the nodes, with short erect branchlets. Leaves opposite crowded, linear, terete-triquetrous, 5-10 mm long, slightly scaberulous; floral leaves similar. Flowers axillary, red, on short thick pedicels. Bracteoles ovate, scarious, brown, mucronate, 2.5-3 mm long. Calyx tube cylindrical, \pm 4 mm long, lobes orbicular, shortly ciliate, \pm 1 mm long. Petals oval-obovate, 2-3 mm long. Stamens and staminodes shortly united at the base. Stamens 0.75 mm long, anthers obovoid. Style slender, \pm 15 mm long, stigma small, subtended by a few cilia. Ovules 8.

Darwinia repens is in the Section Genetyllis and the third group according to Bentham's arrangement, but is quite different from any of the other species.

APIACEAE

Xanthosia tomentosa sp. nov.

Herba perennis ramis pluribus prostratis vel adscendentibus, ad 50 cm longis; stellato-tomentosa, rami demum glabriusculi. Folia in ramis principalibus dispersa, sed in ramulis axillaribus conferta; 10-30 mm longa vel longiora, cuneato-rhomboidea, in petiolis laminibus aequilongis angustata, 3-10-lobata, lobis breviter mucronatis vel acutis, nervis obscuris. Inflo-

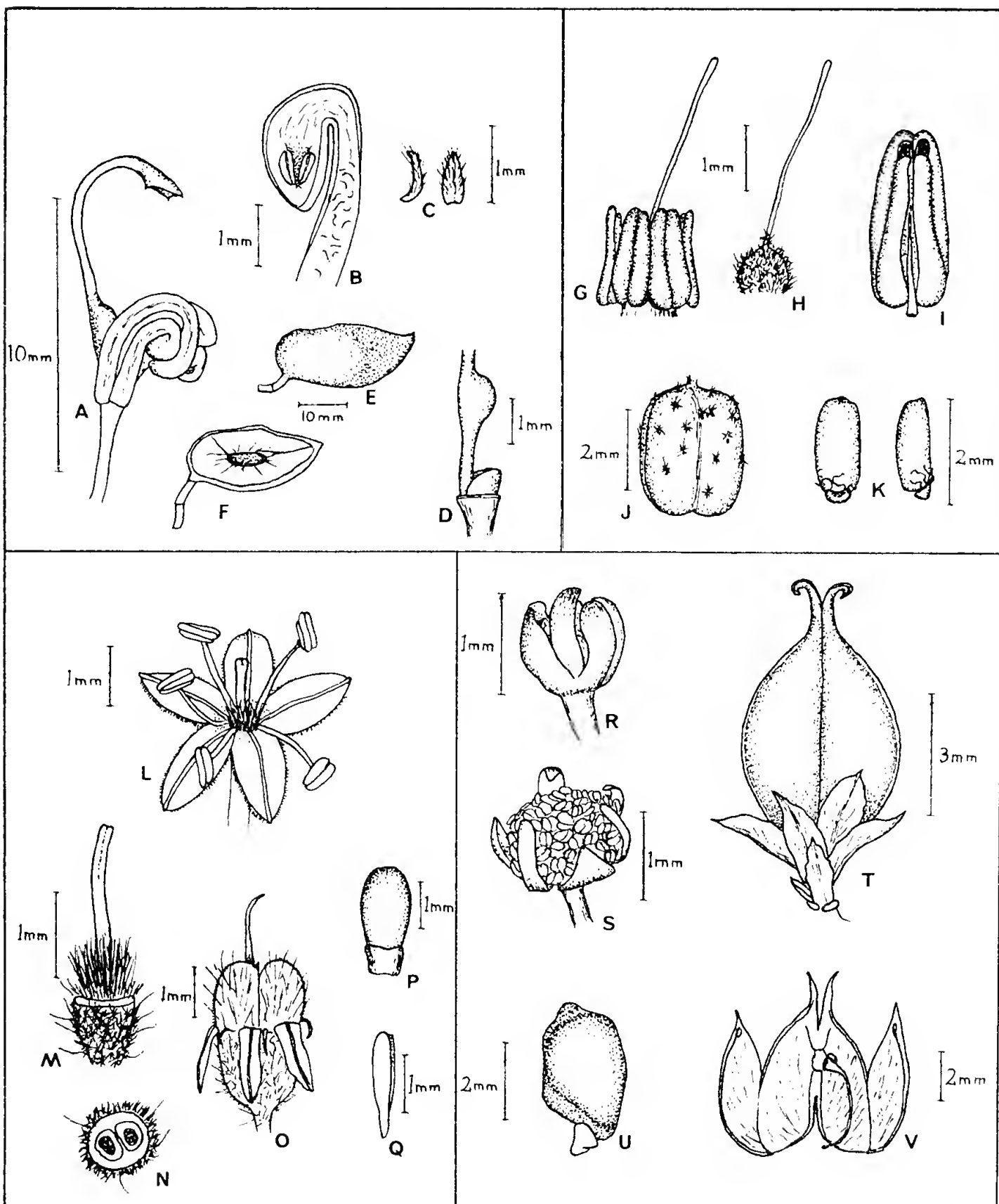


Figure 2.—A-F *Grevillea calcicola*: A. Flower; B. Lower perianth segment, inner view; C. Bracts; D. Ovary and hypogynous gland; E. Fruit; F. Fruit opened, showing seed. A-D from holotype; E, F from Chadwick 1393. G-K *Guichenotia apetala*: G. Stamens surrounding style; H. Ovary and style; I. Anther, inner view; J. Fruit; K. Seeds. G-I from holotype; J, K from Newbey 568. L--Q *Pomaderris bilocularis*: L. Flower; M. Ovary and style; N. T. S. ovary; O. Fruit; P. Seed; Q. Embryo. L-N from George 7355, O-Q from George 7744. R-V *Stachystemon axillaris*: R, S. Male flower; T. Fruit; U. Seed; V. Dehiscent fruit. R, T from George 6828, S. from Havel 177, U, V from George 7814.

rescentia solitaria, terminalia, in pedunculo 3-15 cm longo. Bracteae involucrales 4, 6-9 mm longae, lanceolata-ellipticae, acutae, inderdum lobatae. Bracteae radiatae 4, 15-20 mm longae, ad medium tripartitae, segmentis lateralibus oblique-ovatis, centrale oblanceolata mucronato-acuta. Umbellae 5, floribus ♂ vel ♀. Flores ♀ in pedicellis 0.75-1 mm longis. Calycis tubus 2.5 mm longus; utrumque carpellum latere utroque 3-4-costatum; lobis cordatis, obtusis, < 1 mm longis, glabris. Petali lobos calycis excedentes, inflexi, glabri. Lobi disci prominentes pilis plumosis hirsuti. Styli crassi, \pm 1.7 mm longi. Flores ♂ similes sed minores, pedicellis longioribus, carpellis et stylis rudimentalibus.

Holotype: 2 miles N. of Cockleshell Gully A.S. George 7827a, Sept. 1, 1966.

Perennial herb with many prostrate or ascending stems to 50 cm long, stellate-tomentose, the stems at length more or less glabrous. Leaves scattered on the main stems, but crowded on axillary branchlets, 10-30 mm long, sometimes longer, cuneate-rhomboid, narrowed into petioles as long as the laminae, 3-10 lobed, the lobes shortly mucronate or acute, the nerves obscure. Inflorescence solitary, terminal, on a peduncle of 3-15 cm. Involucral bracts 4, 6-9 mm long, lanceolate-elliptical, acute, sometimes lobed. Ray bracts 4, 15-20 mm long, divided to the middle into 3 segments, the lateral ones obliquely ovate, the central one oblanceolate, mucronate-acute. Umbels 5, the flowers ♂ or ♀. ♀ flowers on pedicels of 0.75-1 mm. Calyx tube 2.5 mm, each carpel 3-4 ribbed on each side; lobes cordate, obtuse, less than 1 mm long, glabrous. Petals exceeding the calyx lobes, inflexed, glabrous. Disc lobes prominent, hirsute with plumose hairs. Styles thick, \pm 1.7 mm long. ♂ flowers similar but smaller, on longer pedicels, with rudimentary carpels and styles.

X. tomentosa is close to *X. rotundifolia* D.C., differing chiefly in the decumbent, many-stemmed habit, the leaf shape and the persistent indumentum (the specific epithet referring to the last character). Other collections are from Mt. Peron, C.A. Gardner 8433 and 10265, and 2 miles E of Diamond Springs, K. Newbey 2353.

EPACRIDACEAE

Styphelia intertexta sp. nov.

Frutex ramosissimus ad 1 m altus ramulis breviter tomentosis. Folia patentia, sessilia, 3-9 mm longa anguste-triangularia ad linearia, acuminata, pungentia, marginibus recurvis; supra glabra, subtus pluri-costata breviter tomentosa pilis inter costas intertextis. Flores albi, axillares, gemini, cum flore rudimentale. Bracteae minimae. Bracteolae 1 mm longae, ovatae, obtusae, leviter carinatae, minute ciliatae. Sepala 3-3.5 mm longa, obtusa, minute ciliata. Corolla 7-9 mm longa; lobi quam tubum longiores, revoluti, intus barbarti etiam faux. superna. Stamina multo exserta. Stylus 6-7 mm longus, glaber vel ad basin breviter pubescens. Ovarium glabrum; discus hypogynus lobatus. Drupa ovoidea, abortu monosperma; endocarpium durum; mesocarpium tenue, in sicco caperatum.

Holotype: 9 miles N. of Ravensthorpe, A.S. George 4431, May 25, 1963.

A much-branched shrub to 1m, the branchlets shortly tomentose. Leaves spreading, sessile, 3-9 mm long, narrow-triangular to linear, acuminate, pungent, the margins strongly recurved; glabrous above, closely several-ribbed below, tomentose, with the hairs interlocking between the ribs. Flowers white, axillary, in pairs with a rudimentary flower. Bracts very small. Bracteoles 1 mm long, ovate, obtuse, minutely ciliate. Sepals 3-3.5 mm long, obtuse, minutely ciliate. Corolla 7-9 mm long; lobes longer than the tube, revolute, bearded on the inner surface and the upper part of the throat. Stamens much exerted. Style 6-7 mm long, glabrous or shortly pubescent towards the base. Ovary glabrous, hypogynous disc lobed. Drupe ovoid, 1-seeded by abortion; endocarp hard; mesocarp thin, somewhat wrinkled when dried.

Belonging to the Section *Soleniscia*, the species is closest to *S. melaleucoides* F. Muell, from which it chiefly differs in the convex, strongly recurved leaves with tomentose ribs on the lower surface. The specific epithet refers to the interlocking hairs between the ribs.

Other collections are from 10 miles E. of Ongerup, K. Newbey; \pm 30 miles W. of Ravensthorpe, A.S. George 7073 (in fruit); Mt. Short, N. of Ravensthorpe, A.S. George 4443; Grass Patch, C.F. Davies 230; Grass Patch, C.J. Rhind 7; N. of Bullabulling, J.S. Beard 3348; and 3 km SE of Queen Victoria Spring, D.W. Goodall 2946.

The collection by Beard has glabrous branchlets and the undersurface of the leaves tomentose only between the ribs. The sepals are 2 mm long, and the corolla tube about 2 mm longer than the sepals. The Goodall collection has less revolute leaves than normal, also tomentose only between the ribs. The flowers are slightly smaller but quite typical morphologically.

CONVOLVULACEAE

Ipomoea yardiensis sp. nov.

Frutex multicaulis ad 1.5 m altus, dense velutinus pilis intricatis. Rami crassi haud volubiles, sine succo lacteo. Folia petiolata late-orbicularia, obtusa vel parum emarginata; petiolus 0.5-3 cm longus, lamina 2-7 cm, penninervis. Flores 1-3 in pedunculis axillares 5-15 mm longos. Bracteae obtusae deciduae, 2-3 mm longae. Pedicelli 5-10 mm longi. Sepala ovata, obtusa, subaequalia 8-11 mm longa, ad basin cum 2 glandibus oblongis glabris, extus tomentosa praeter sepalorum interiorum marginibus glabris, intus omnino glabra. Corolla infundibuliformis, 4-7 cm longa, rosea glabra praeter taenias mid-petalinas extus tomentosas. Stamina stylusque inclusus. Filamenta inaequalia, ad basin dilatata, hirsuta; anthera 5-7 mm longa. Stylus glaber; stigmata 2, globosa. Ovarium glabrum biloculatum, loculis bi-ovulatis. Calyx fructifer parum auctus; fructus capsularis, globosus, ad basin 4-valvatus. Semina dense sericeo-villosa, 8 mm longa.

Holotype: 3 miles S. of Yardi Creek homestead, on rocky limestone rises at western edge of Cape Range, A.S. George 6617, May 26, 1965.

A many-stemmed shrub to 1.5 m tall, densely tomentose with a close indumentum of intricate woolly hairs. Stems thick, never twining, with-

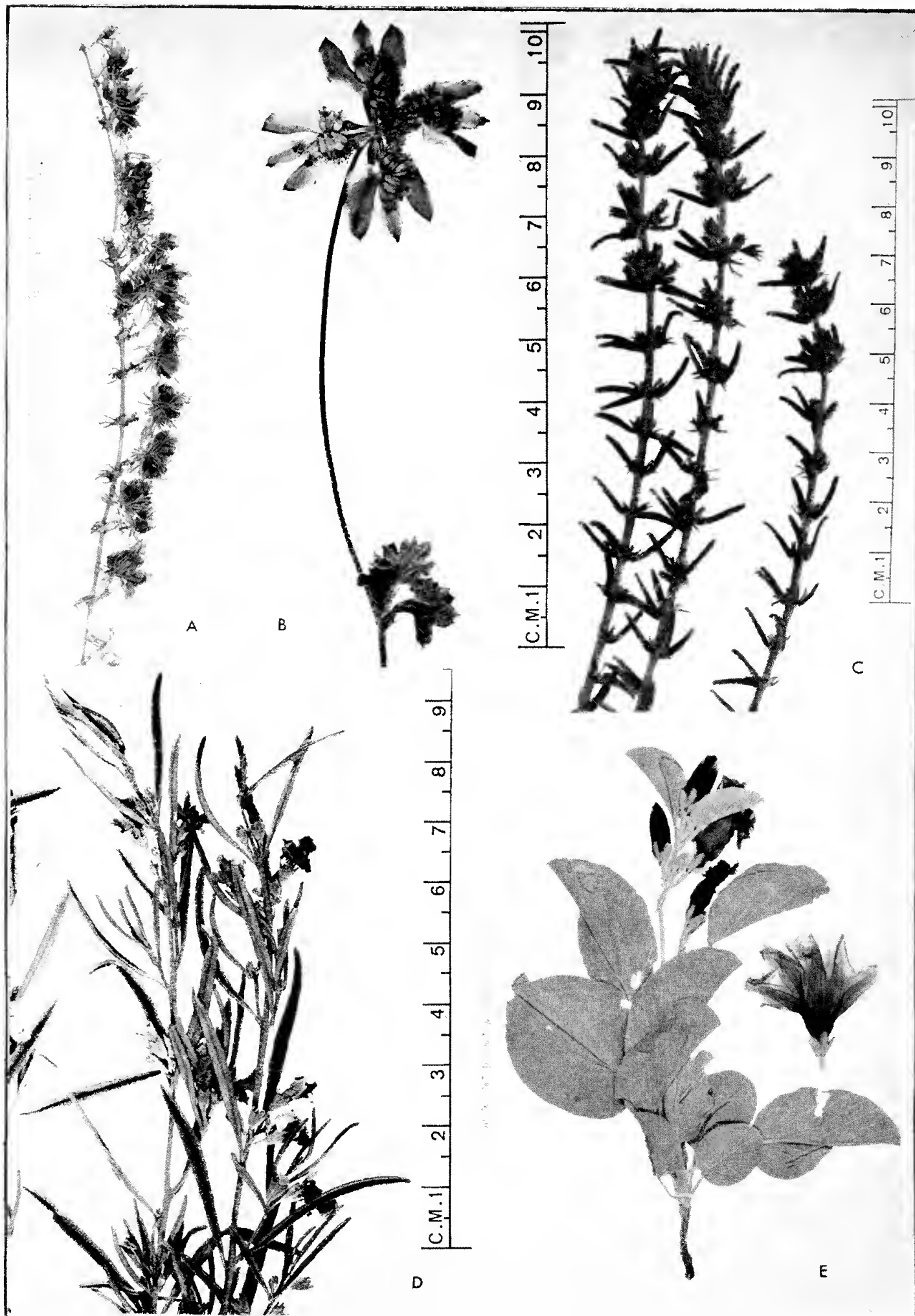


Figure 3.—All photographs from type collections. A. *Darwinia repens* sp. nov.; B. *Xanthosia tomentosa* sp. nov.; C. *Pityrodia scabra* sp. nov.; D. *Pityrodia canaliculata* sp. nov.; E. *Ipomoea yardiensis* sp. nov.

out milky sap. Leaves petiolate, broadly orbicular, obtuse or slightly emarginate; petioles 0.5-3 cm long, blade 2-7 cm, penninerved. Flowers 1-3 on axillary peduncles 5-15 mm long. Bracts obtuse, deciduous, 2-3 mm long. Pedicels 5-10 mm long. Sepals ovate, obtuse, subequal, 8-11 mm long, with a narrow oblong glabrous gland on each side at the base, tomentose outside, the inner ones with glabrous margins, all glabrous within. Corolla funnel-shaped, 4-7 cm long, bright pink, darker in the tube, glabrous except the mid-petaline bands which are tomentose outside. Stamens and style included. Filaments unequal, dilated and hirsute at the base; anthers 5-7 mm long. Style glabrous, stigmata 2, globular. Ovary glabrous, 2-celled with 2 ovules per cell. Fruiting calyx slightly enlarged. Fruit a globular capsule, the 4 valves splitting to the base. Seeds densely silky-villous, 8 mm long.

So far as can be ascertained in the absence of a full revision of the genus, this species appears to be closest to the American *I. crassicaulis* (Benth.) B.L. Robinson, of the Section *Eriospermum*.

It is known only from, or close to, Yardie Creek Station, south of North West Cape. The fruit is described from a specimen collected near North West Cape by W.H. Butler in Sept. 1963.

DICRASTYLIDACEAE

Pityrodia canaliculata sp. nov. Sect. *Depremesnilia*

Frutex multicaulis ad 2 m altus indumento arcto squamarum peltatarum minute ciliatarum. Folia opposita 1.5-5 cm longa, linearia, obtusa, breviter petiolata, canaliculata-carinata, superne olivacea demum glabra, subtus laevia paulo reticulata, marginibus planis vel leviter recurvibus. Flores axillares pedicellati solitarii vel breviter cymosi. Bracteae minimae. Calyx 3.5-4 mm longus, paulo angulatus; extus squamatus; lobi triangulares 1-1.5 mm longi marginibus incurvis, intus lobis paulo hirsutis tubo glabro. Corolla alba, fauce rufo-maculata, 8-9 mm longa tubo quam calyce longiore, bilabiata; labium superum lobis 2, obtusis, infernum longius 3-lobatum, lobo medio quam aliis majore; corolla extus praeter basin squamata, intus infra medium annulata-barbata, labio inferno pubescente. Stamina paulum exserta; anthera breviter apiculata. Stylus glaber. Ovarium ad apicem hirsutum.

Holotype: 19 miles W. of Sandstone, A.S. George 7992, Sept. 12, 1966.

A many-stemmed shrub to 2 m with a close indumentum of peltate, minutely ciliate scales. Leaves opposite, 1.5-5 cm long, linear, obtuse, shortly petiolate, canaliculate-carinate, dark green and becoming glabrous above, pale below and somewhat reticulate, margins flat or very slightly recurved. Flowers axillary, pedicellate solitary or shortly cymose. Bracts very small. Calyx 3.5-4 mm long, somewhat angular, covered with scales outside; lobes deltoid, 1-1.5 mm long, the margins incurved, inside, the lobes slightly hirsute, the tube glabrous. Corolla white with reddish spots in the throat, 8-9 mm long, the tube exceeding the calyx, bilabiate; upper lip of 2 obtuse lobes, lower lip longer, 3-lobed,

the central lobe larger than the others; corolla covered with scales outside except at the base, inside with a dense ring of simple hairs below the middle and pubescent on the lower lip. Stamens slightly exserted; anthers shortly apiculate. Style glabrous. Ovary hirsute on top.

The species is closest to *P. lepidota* (F. Muell) E. Pritzel, differing chiefly as follows: habit much taller; indumentum of less ciliate scales; leaves longer, canaliculate, becoming glabrous above; flowers on longer pedicels; corolla less densely hirsute inside; ovary hirsute only on top; style glabrous.

The specific epithet refers to the leaves.

Pityrodia scabra sp. nov. Sect. *Chloanthopsis*

Frutex \pm 1 m altus, indumento viscido, aureo pilorum ramosorum. Folia 3-verticillata, 0.5-1.2 cm longa, linearia, obtuse, sessilia, marginibus revolutis \pm crenulatis ut bullatis videntur; grosse tomentosa supra demum scabra. Flores axillares breviter cymosa. Bracteolae lineares. Calyx 5 mm longus, glanduloso-pubescent, lobis quam tubum paulum brevioribus, involutis costis mediis prominentibus. Corolla 7-8 mm longa, tubo angusto quam lobis longiore; labium superum obtuse-lobatum, infernum longius, 3-lobatum, lobo mediis quam aliis majore; faux ad basin filamentorum etiam secus lobum medium infernum hirsutum; corolla aliter glabra. Stamina breviter exserta; anthera breviter appendiculata. Stylus glaber. Ovarium dense hirsutum, ovulis per funiculos breves affixis; discus hypogynus paulum lobatus.

Holotype: Cowcowing, S.B. Rosier 27, Aug. 1959.

Shrub \pm 1 m tall, with a viscid, golden indumentum of branched hairs. Leaves in whorls of 3, 0.5-1.2 cm long, linear, obtuse, sessile, margins revolute, \pm crenulate so as to appear bullate; coarsely tomentose, becoming scabrous above. Flowers axillary, shortly cymose. Bracteoles linear. Calyx 5 mm long, glandular-pubescent, lobes slightly shorter than the tube, involute with prominent midribs. Corolla 7-8 mm long, the tube narrow, longer than the lobes; upper lip of 2 obtuse lobes, lower lip 3-lobed, the central one larger than the others; throat hirsute around the base of the filaments and along the lower mid-lobe; corolla otherwise glabrous. Stamens shortly exserted; anthers shortly appendiculate. Style glabrous. Ovary densely hirsute, the ovules attached to short funicles; hypogynous disc slightly lobed.

The species appear closest to *P. hemigenioides* (F. Muell.) Benth. However the coarse viscid indumentum gives it an entirely distinct appearance; further differences are the larger whorled leaves with somewhat bullate margins and the flowers in small cymes.

The epithet refers to the rough surface remaining on the leaves as the indumentum wears off.

The holotypes of the ten species described above will be deposited in the Western Australian Herbarium, Perth. Isotypes of all except *Grevillea calcicola* will be distributed to the National Herbarium of Victoria, Melbourne, and the Royal Botanic Gardens, Kew.

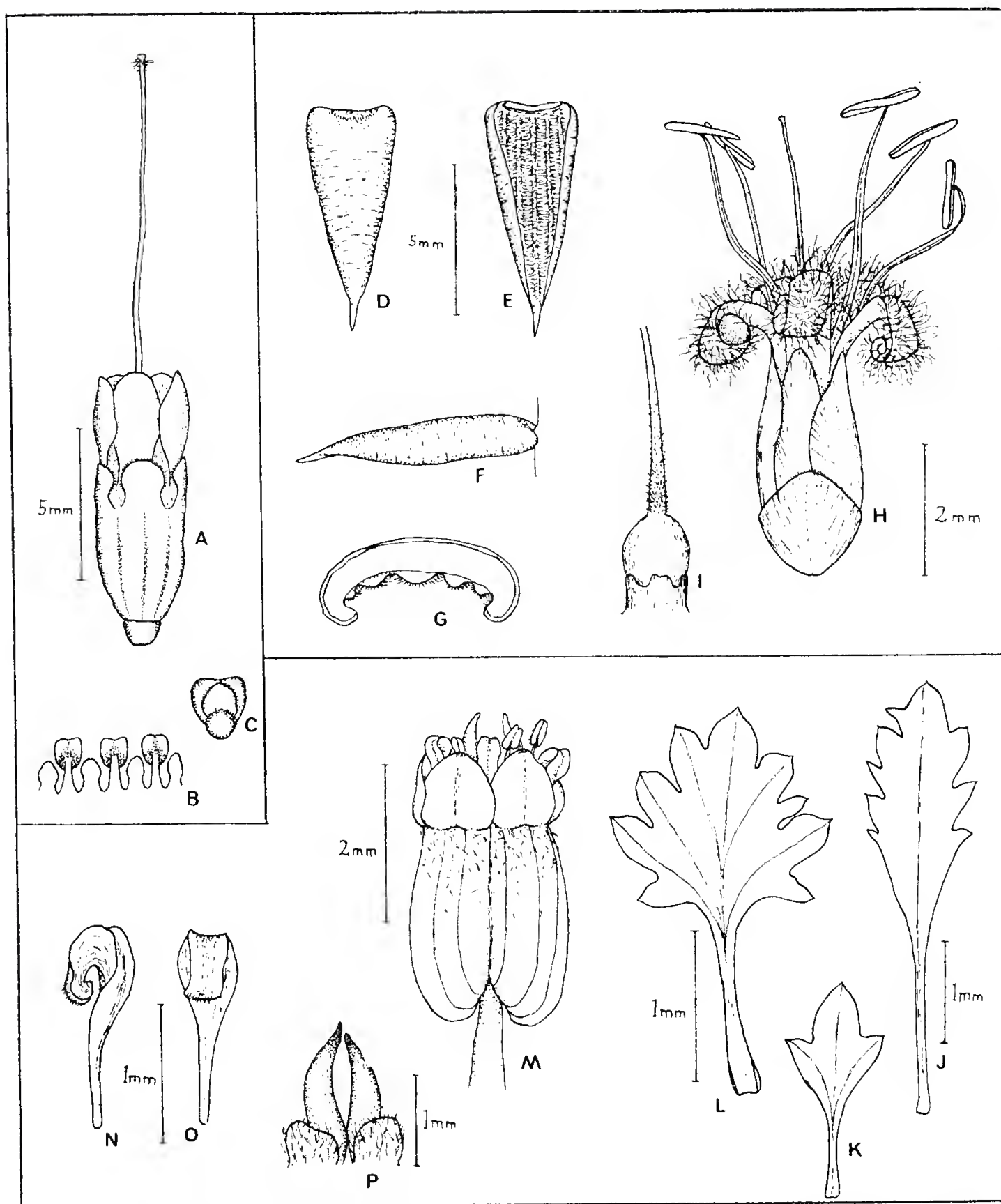


Figure 4.—A-C *Darwinia repens*; A. Flower; B. Three stamens, with staminodia; C. Anther. All from holotype. D-I, *Styphelia intertexta*: D, E, F. Three views of leaf; G. T.S. leaf; H. Flower; I. Ovary, with lower part of style and hypogynous disc. All from holotype. J-P *Xanthosia tomentosa*: J. Leaf from Gardner 8433; K. Small leaf from George 7827b; L. Leaf; M. Flower; N, O. Side and inner view of petal; P. Styles and lobes of disc. L-P from holotype.

13.—A preliminary account of the vegetation of Loch McNess, a swamp and fen formation in Western Australia

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Abstract

Loch McNess is a body of fresh, alkaline water situated in the Yanchep National Park, Western Australia. It is extensively overgrown by vegetation, and sedge swamp and sedge fen formations can be recognised, which are similar floristically and structurally to those in other Australian States and abroad. These formations are bordered by communities dominated by *Melaleuca* or *Banksia*.

Introduction

The purpose of this communication is to describe the vegetation associated with Loch McNess, a body of fresh water situated in the Yanchep National Park (Jenkins 1964; Jenkins *et al.* 1964). The region studied lies in a depression some 31 miles to the north of Perth, and four miles from the coast, where the annual rainfall is about 27 inches (Little 1965). The depression is in limestone country, and may be a karst feature formed by the collapse of underground caverns (McArthur and Bettenay 1960). The general features of the area are depicted in Figure 1, and the distribution of the main types of vegetation is shown in Figure 2.

The area investigated may be divided into three sections. The eastern section, of 40 acres, is extensively overgrown with sedge communities and contains little open water. It has been variously interfered with, the aerial photographs revealing "cropping marks" which result from attempts in the 1930's to establish playing fields†. The limestone ridge to the east contains caves which are of considerable local interest, and water drains from this region through the eastern, and into the southern section of the Loch. The southern section, some 66 acres, consists largely of open water as described in the first published account of "Lake Yanchep", as it was then known (Milligan 1903). Part of the area was deepened by dredging between 1936 and 1940; rowboats may be hired, and a launch takes visitors around the dredged channel at the periphery of the open water.

The extensive northern section, 375 acres, is largely covered with vegetation, as noted by Milligan (1903). The northern and southern sections are separated by a region of shallow water, across which silt and earth were dumped in the late 1930's and again in the 1950's to form a causeway. A shallow channel exists near to the western end of the causeway, and a bridge was partly constructed across this channel in about 1939, but never completed. *Melaleuca* trees, present girth at breast height up to 113 cm were not cleared from the ap-

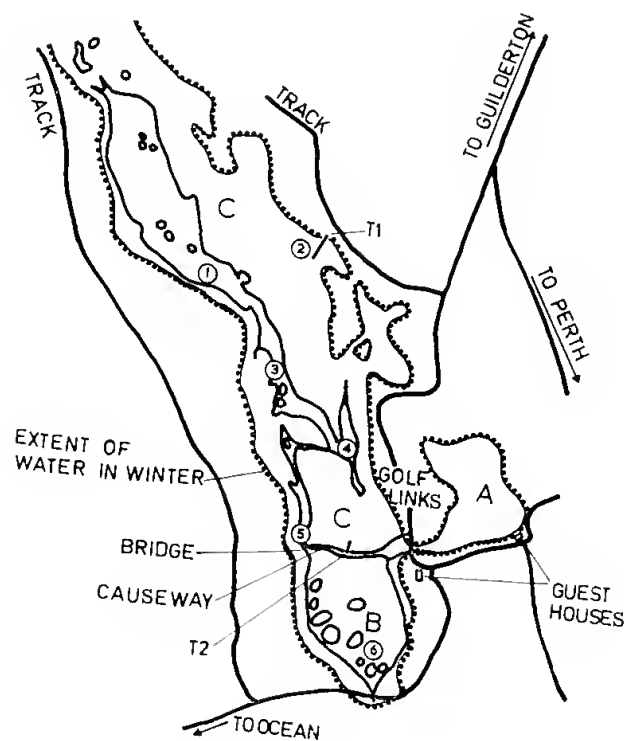


Figure 1.—The general features of Loch McNess, drawn from an aerial photograph. A, B, and C are the eastern, southern, and northern sections respectively. The numbers 1 to 6 represent the sites from which water samples were taken for pH and resistance measurements. T₁ and T₂ are the sites of the transects depicted in Figure 5 and Figure 6 respectively.

proaches to the bridge. Access to the northern section may be had by boat from the south, though even in winter progress is greatly impeded by sedges and shallow water, the channels in some regions being narrow and difficult to locate. A track suitable for four-wheel-drive vehicles runs parallel to each side of the northern section, but the fringing vegetation makes access to the water difficult. The northern section has been burned, at least in part, every three to four years since about 1940, in an effort to check the growth of vegetation.

Description

Open water.—The three sections include approximately 134 acres of open water. Water drains into the Loch from the surrounding limestone hills, and overflows into caves at the southern end and at least one point in the northern section. The water level is fairly constant, but may rise by some 20 cm. above the normal level in an exceptionally wet season‡. No movement could be seen in the water apart from a gentle flow between the eastern and southern sections, and at the point where water drains from the Loch to the south.

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† We are indebted to the Secretary of the National Parks Board for the historical information included in the paper.

‡ Information supplied by the Secretary of the National Parks Board.

Samples of water were collected in September from the sites indicated by the numbers 1-6 in Figure 1, and transferred to the laboratory for measurements of pH and electrical resistance, using a Pye pH meter and a Metrohm Conductivity Apparatus. Results are presented in Table 1, along with data for Perth tap water and sea water. The water is alkaline and fresh. Even within the sedge communities of the northern section, 320 metres from open water, the pH was not lower than 7.6.

The water is on the whole remarkably clear, though often cloudy in the southern section, where boating disturbs the bottom. In the northern section the water in winter is typically 20 to 50 cm deep in open regions, and the smooth, greenish-grey bottom appears deceptively firm. However, every movement of an oar lifts a cloud of black, loosely-compacted organic debris to drift slowly and settle gently, and it is possible to sink an oar vertically into this deposit to a depth of 80 cm without effort. A sample of the upper 5 cm of deposit was found to consist of many fragments of epidermis

and other plant debris, small dark particles taken to be at least in part fragments of charcoal, diatom frustules, a few strands of blue-green algae and *Spirogyra*, unicellular green algae and Protista. Diatoms and blue-green algae were much more prevalent in a bottom sample taken from beneath water sheltered by *Melaleuca* trees.

TABLE 1

Estimates of pH and electrical resistance of water samples from Loch McNess. The numbers correspond with the sites shown in Figure 1. Tap water and sea water are included for comparison.

Sample				pH	Resistance (Ohms)
1	Northern section	7.7
2	Northern sedge community	7.6
3	Northern section	8.1	1620
4	Northern section	7.6	1670
5	Near bridge	7.6	1770
6	Southern section	8.0	1850
University tap water					1320
Sea water					20

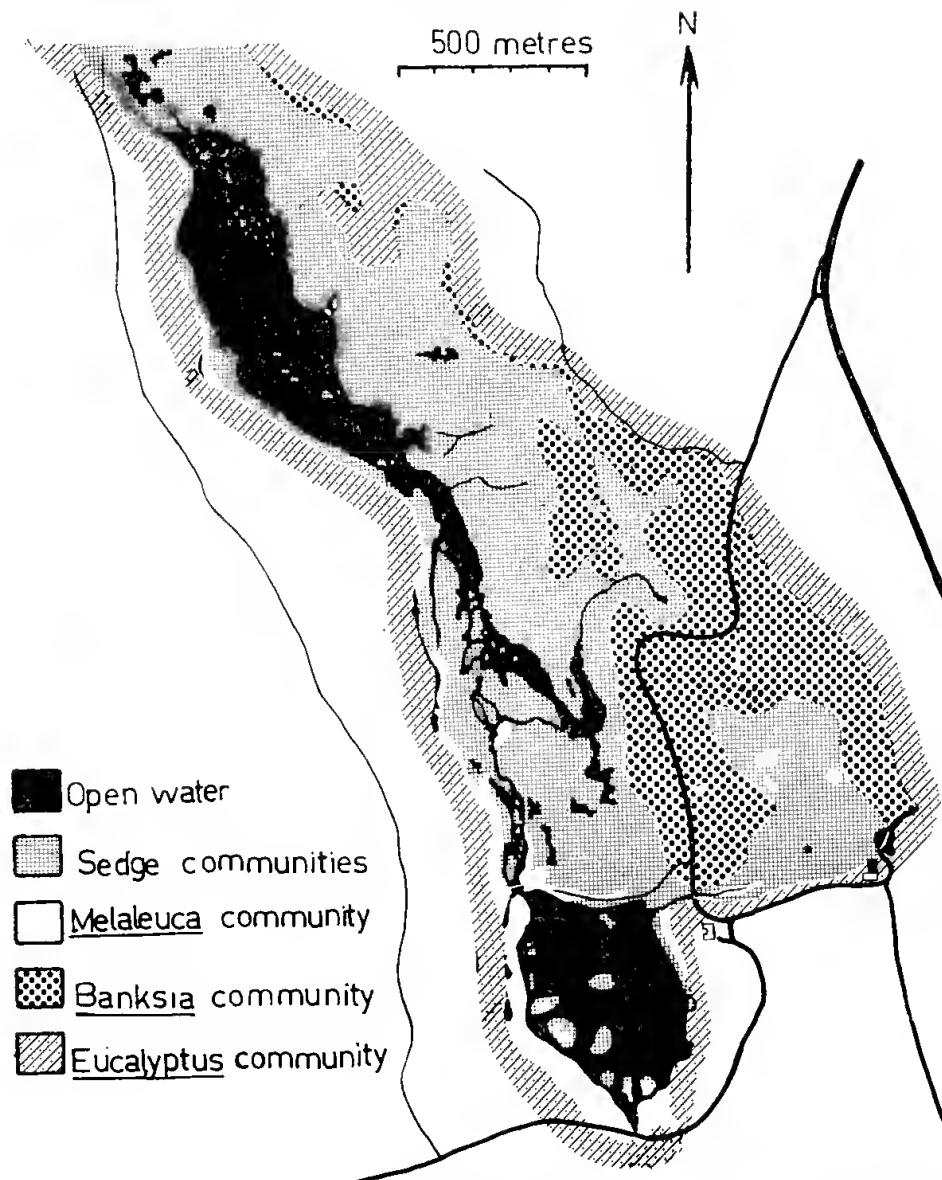


Figure 2.—The general distribution of vegetation in the Loch McNess region, compiled from an aerial photograph and field observations. The extent of the *Eucalyptus* woodland is not shown.

Occasionally drifts of *Spirogyra* are observed, and in some regions there occur small patches of *Chara*, usually densely covered with *Spirogyra*. No aquatic vascular plants were observed in the open water, though the floating *Lemna minor* occurs in the sedge communities, and *Azolla* and *Spirodela* have been recorded for the area (Smith and Marchant 1961).

Species present.—A list of the vascular species encountered is presented in Table 2, and a collection of the sedge species has been incorporated into the Herbarium of the Botany Department, University of Western Australia. Species which occur only in the *Banksia littoralis* and *Eucalyptus gomphocephala* communities have not been included in the table. The plants known to be introduced to the State were collected exclusively from the disturbed southern and eastern sections.

TABLE 2

Vascular plants recorded from Loch McNess.

PTERIDOPHYTA	
	Polypodiaceae
<i>Pteridium esculentum</i> (Forst. f.) Nakai	
	Azollaceae
* <i>Azolla filiculoides</i> Lam.	
ANGIOSPERMAE	
	Monocotyledoneae
	Cyperaceae
<i>Carex appressa</i> R. Br.	
<i>Carex fascicularis</i> Sol. ex Boott (formerly included in <i>Carex pseudocyperus</i> L.)	
<i>Cladium arthrophyllum</i> (Nees) F.v.M.	
<i>Cyperus tenuiflorus</i> Rottb. (formerly included in <i>Cyperus rotundus</i> L.)	
<i>Gahnia trifida</i> Labill.	
<i>Lepidosperma drummondii</i> Benth.	
<i>Lepidosperma gladiatum</i> Labill.	
<i>Lepidosperma longitudinale</i> Labill.	
<i>Machaerina articulata</i> (R. Br.) Koyama (= <i>Cladium articulatum</i> R. Br.)	
<i>Machaerina juncea</i> (R. Br.) Koyama (= <i>Cladium junceum</i> R. Br.)	
<i>Machaerina laxa</i> (Nees) Koyama (= <i>Cladium laxum</i> (Nees) Benth.)	
<i>Schoenus andrewsii</i> W. V. Fitzg.	
<i>Schoenus indutus</i> (F.v.M.) Benth.	
<i>Schoenus rodwayanus</i> W.V. Fitzg.	
<i>Schoenus unispiculatus</i> (F.v.M.) Benth.	
<i>Scirpus cernuus</i> Vahl.	
<i>Scirpus nodosus</i> Rottb.	
<i>Scirpus validus</i> Vahl. (formerly included in <i>Scirpus lacustris</i> L.)	
	Iridaceae
<i>Patersonia occidentalis</i> R. Br.	
	Juncaceae
<i>Juncus bufonius</i> L.	
<i>Juncus capitatus</i> Weig.	
<i>Juncus pallidus</i> R. Br.	
<i>Juncus planifolius</i> R. Br.	
	Lemnaceae
<i>Lemna minor</i> L.	
* <i>Spirodela oligorrhiza</i> (Kurz) Hegelm.	
	Liliaceae
<i>Wurmbea dioica</i> (R. Br.) F.v.M.	
	Orchidaceae
<i>Diuris pauciflora</i> R. Br.	
<i>Thelymitra pauciflora</i> R. Br.	
	Poaceae
† <i>Arundo donax</i> L. var. <i>versicolor</i> (Miller) Stokes	
† <i>Cortaderia argentea</i> (Nees) Stapf.	
<i>Cynodon dactylon</i> (L.) Pers.	
† <i>Holcus lanatus</i> L.	
† <i>Paspalum dilatatum</i> Poir	
† <i>Polypogon monospermiensis</i> (L.) Desf.	
<i>Sporobolus actinocladius</i> (F.v.M.) F.v.M.	
	Restionaceae
<i>Lepyrodia muii</i> F.v.M.	
<i>Loxocarya flexuosa</i> (R.Br.) Benth.	
	Scheuchzeriaceae
<i>Triglochin procera</i> R. Br.	
<i>Triglochin striata</i> Ruiz. et Pav.	

† Introduced species.

* Recorded by Smith and Marchant (1961) but not seen during the present survey.

	Typhaceae
<i>Typha angustifolia</i> L.	
	Xanthorrhoeaceae
<i>Xanthorrhoea preissii</i> Endl. in Lehm.	
	Dicotyledoneae
	Aizoaceae
<i>Carpobrotus aequilaterus</i> (Haw.) N. E. Brown	
	Apiaceae
<i>Apium australe</i> Thou.	
<i>Centella asiatica</i> (L.) Urb.	
	Asteraceae
<i>Cotula coronopifolia</i> L.	
<i>Embergeria megalocarpa</i> (Hook f.) Boulus (= <i>Sonchus megalocarpus</i> (Hook f.) Black)	
<i>Senecio aff. lautus</i> Forst. f. ex. Willd.	
	Chenopodiaceae
<i>Rhagodia preissii</i> Moq.	
	Geraniaceae
† <i>Geranium molle</i> L.	
<i>Pelargonium capitatum</i> (L.) L'Herit ex Ait.	
	Goodeniaceae
<i>Dampiera trigona</i> De Vriese	
<i>Scaevola nitida</i> R. Br.	
	Haloragaceae
<i>Haloragis brownii</i> (Hook f.) Schindler	
	Lauraceae
<i>Cassytha racemosa</i> Nees	
	Mimosaceae
<i>Acacia cyanophylla</i> Lindl.	
	Myoporaceae
<i>Myoporum tetrandrum</i> (Labill.) Domin (= <i>Myoporum serratum</i> R. Br.)	
	Myrtaceae
<i>Eucalyptus rudis</i> Endl.	
<i>Melaleuca raphiophylla</i> Schau.	
	Onagraceae
<i>Epilobium billardierianum</i> Ser. (formerly included in <i>Epilobium glabellum</i> (Forst f.) Black)	
	Papilionaceae
† <i>Psoralea pinnata</i> L.	
<i>Templetonia retusa</i> (Vent.) R. Br.	
<i>Viminaria denudata</i> Sm.	
	Polygalaceae
<i>Comesperma virgatum</i> Labill.	
	Polygonaceae
<i>Polygonum serrulatum</i> Lag.	
	Proteaceae
<i>Banksia littoralis</i> R. Br.	
	Ranunculaceae
<i>Ranunculus lappaceus</i> Sm.	
	Rhamnaceae
<i>Trymalium spathulatum</i> (Labill.) Ostf.	
	Rutaceae
<i>Phetaliu anceps</i> D.C.	

As can be seen from the table, sedges make up a large proportion of the species; there are 18 Cyperaceae, as compared with four Juncaceae, the family which has the second-largest number of native species present. Of these four Juncaceae none is abundant, and *Juncus pallidus*, *J. bufonius* and *J. capitatus* are limited to the disturbed southern regions. In contrast, sedges dominate some 315 acres of the vegetation.

Vegetation fringing open water.—The sedge communities encroach upon the open water from the margins. Several important fringing species are encountered, but *Scirpus validus* is by far the most common, and forms very dense mats of vegetation in the northern section (Fig.3). Where the water is shallow, it appears that the rhizomes grow out more rapidly under the surface of the organic debris, forming less dense stands, *Lepidosperma drummondii* is also a common fringing species, often occurring between stands of *Machaerina articulata* and open water (Fig.4), but only rarely between *Scirpus validus* and open water. *Machaerina juncea* and *Machaerina laxa* are also present as fringing species, and in some regions of deeper water may build up protruding shelves of densely packed rhizomes. In the extreme southern area



Figure 3.—*Scirpus validus* fringing open water in the northern section. The tips of the culms are approximately 1.5 metres above the water level. The water is 20 cm deep. In the background can be seen further stands of *Scirpus validus*, with *Viminaria denudata* and *Eucalyptus gomphocephala* behind.



Figure 4.—Open water fringed by a narrow band of *Lepidosperma drummondii* with, behind, dense stands of *Machaerina articulata*. The *Machaerina* tips rise some 2.5 metres above water, which is 20 cm deep.

of the Loch a community of *Melaleuca raphiophylla* occurs at the edge of the main body of open water.

Vegetation of the sedge communities.—The large areas labelled in Figure 2 as “sedge communities” consist of a complex mosaic of vegetation, variously dissected by pools and sluggish waterways. Profile drawings of transects running into typical areas of sedge vegetation illustrate

this complexity (Figs 5 & 6). Within the sedge communities regions of deeper water, some 40 cm in winter, are occupied by dense stands of *Scirpus validus* and *Machaerina articulata* (Fig 5). Some regions are richer in species. For example north of the causeway (Fig. 6), where the water level is 30 cm in winter, but at or below ground level by the end of summer, *Typha angustifolia*, *Machaerina laxa* and *Machaerina*

juncea are also common, and there are small patches of more-or-less open water. *Machaerina juncea* forms meadows in regions where the water is even more shallow in winter (7 cm on the transect line, Fig.5). The meadows are typically 70 cm tall, and the density of living culms was estimated from one quadrat to be 4,400 per square metre. In these meadows shrub species are established, and even seedlings of *Banksia littoralis* (Fig.7).

Lepidosperma gladiatum grows very prolifically in some regions, especially towards the border between the sedge communities and the adjacent woodland (Fig.5), where it may form pure stands up to three metres in height, which are quite impenetrable. The species also occurs on adjacent land, and in water to a depth of approximately 50 cm in winter.

The fringing Melaleuca community.—*Melaleuca raphiophylla* dominates a narrow community fringing some areas of sedge vegetation, particularly in the southern section (Fig. 2), where it may be associated with *Eucalyptus rudis*. The transect depicted in Figure 6 passes through a narrow fringe of *Melaleuca*. It can be seen that *Melaleuca* seedlings become established among the sedges and, if they are not killed by fire, presumably survive to extend the *Melaleuca* community. The seedlings appear quite vigorous but are few in number. Beneath the trees species of the sedge communities are eliminated, presumably because of shading. The *Melaleuca* trees also occur on soil which is just below or above the winter water level, and in these regions *Gahnia trifida* is common, while *Polygonum serrulatum* occurs in sheltered pools.

Other fringing communities.—The higher land surrounding the Loch carries a woodland dominated by *Eucalyptus gomphocephala* D.C. The banks of the Loch rise more steeply on the western side, and the *Eucalyptus* is there separated from the sedge vegetation by a fringe of *Melaleuca* or shrubs such as *Viminaria*. The slope of the eastern bank is more gentle, and the *Eucalyptus* woodland is separated from the sedge vegetation by a woodland of *Banksia littoralis*. Part of a *Banksia* community is included in Figure 5. In this community occur many large plants of *Xanthorrhoea preissii*, which are particularly common near to the border of the sedge vegetation. The trunks of the *Banksia* and *Xanthorrhoea* plants are fire scarred.

Discussion

A comparison of Loch McNess with similar formations in other temperate regions.—The sedge communities of Loch McNess may be divided into two distinct types. Firstly, there is the swamp vegetation, occurring in the deeper water, and characterised by *Scirpus validus* and *Machaerina articulata*. Secondly, there are the "sedge meadows" dominated by *Machaerina juncea*, in which the water level is just above the peat surface in winter, and below the surface in summer; this formation, comprising sedge and alkaline peat, is a true fen (Tansley 1939). The general appearance of the vegetation is very similar to that of swamp and fen formations in other parts of the world (Weaver and Clements

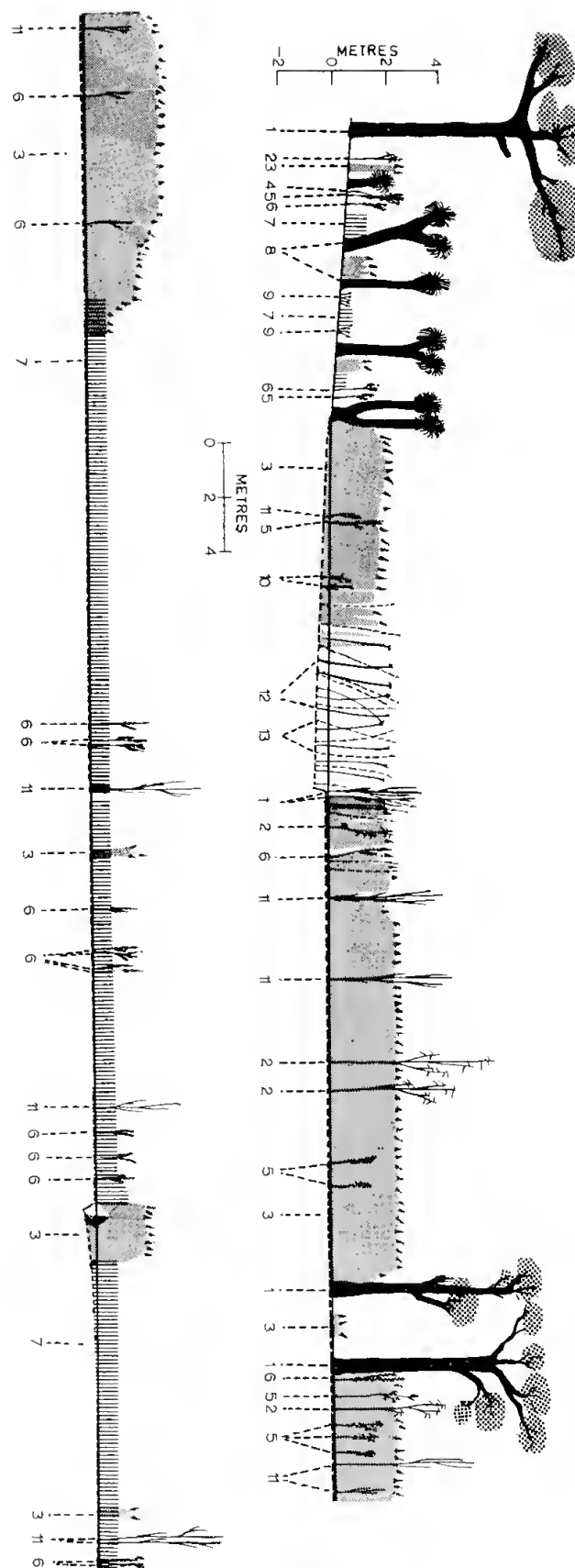


Figure 5.—Profile drawing made from a transect through *Banksia* and sedge communities. The transect was one metre wide, and in the position T₁, Fig. 1. No attempt has been made to indicate the number of sedge culms. Key to species: 1. *Banksia littoralis*, 2. *Acacia cyanophylla*, 3. *Lepidosperma gladiatum*, 4. *Harndenbergia comptoniana*, 5. *Templetonia retusa*, 6. *Phebalium anceps*, 7. *Machaerina juncea*, 8. *Xanthorrhoea preissii*, 9. *Scirpus nodosus*, 10. *Machaerina laxa*, 11. *Viminaria denudata*, 12. *Scirpus validus*, 13. *Machaerina articulata*. Zero on the vertical scale represents the water level in winter.



Figure 6.—Profile drawing made from a transect through *Melaleuca* and sedge communities. The site of the transect is marked T₂ in Fig. 1. The transect was one metre wide except for the *Melaleuca* trees, which were approximately two metres from the transect lines. No attempt has been made to indicate the number of sedge culms. Key to species: 1. *Acacia cyanophylla*. 2. *Melaleuca raphiophylla*. 2. *M. raphiophylla*, moribund. 3. *Machaerina juncea*. 4. *Triglochin procera*. 5. *Machaerina laxa*. 6. *Polygonum serrulatum*. 7. *Typha angustifolia*. 3. *Scirpus validus*. Zero on the vertical scale represents the water level in winter.

1938; Tansley 1939; Pidgeon 1940; Eardley 1943; Martin 1960a,b). In addition, it is probable that the *Melaleuca* community is analagous with the "carr" of the European fenlands (Tansley 1939; Eardley 1943).

Among the species occurring naturally at Loch McNess there is 35% endemism, as compared with approximately 75% for the flora of the south-west vegetation province of Western Australia (Gardner 1959), emphasising the general observation that swamps and fens characteristically include species of cosmopolitan distribution (Diels 1906; Muenscher 1944). Eardley (1943) presents a table in which species occurring in the Eight-mile Creek Swamp of South Australia are matched against comparable species for Europe and North America, while Martin (1960b) includes, in his account of the South African Groenvlei, a similar comparison between the species of Groenvlei and those of Europe. Data from these two tables are included in Table 3 for comparison with species at Loch McNess. The floristics of Loch McNess are

clearly quite similar to those of Eight-mile Creek, where 24% of the Loch McNess species, and 38% of the genera, also occur.

Table 3 also includes prominent species of cosmopolitan distribution, which are not represented in Loch McNess. Of these, *Eleocharis acuta* and *Scirpus americanus* may well prove to be present, since they are recorded for the State (Blackall 1954). The absence of *Phragmites communis* is of some interest. This species, although of cosmopolitan distribution, and stated in Floras of other States as being present "throughout Australia", is in fact not native to the State. Gardner (1952) notes that it has been recorded at Albany, where it is apparently introduced. (*Phragmites karka* (Retz.) Trin. ex Steud. occurs in the north of the State.) *Cladium procerum* is also absent from the State.

Viminaria denudata is common at Loch McNess, but absent from Eight-mile Creek, even though it is present in neighbouring South Australian swamps. Eardley suggests that high pH may preclude the species, but its occurrence at Loch McNess does not support this suggestion, since the pH of the two regions is very similar. *Lepidosperma gladiatum* is also a prominent species at Loch McNess, but absent from Eight-mile Creek, though present in South Australia. It seems quite possible that the dense fringing stands of this species at Loch McNess are favoured by burning; Eight-mile Creek Swamp had not been burned before the vegetation survey, though it has since been drained and cleared (Eardley 1943).

Plant succession at Loch McNess.—In general, succession in vegetation associated with fresh-water lakes proceeds from open water to swamp community, then to fen, which is invaded by fen "carr", and finally woodland (e.g. Tansley 1939). Although it is not possible to draw definite conclusions from the present preliminary examination of the Loch McNess vegetation, it does appear that the succession follows this general pattern, and the following suggestions may reasonably be made. It is clear that no, or extremely few, plants are able to invade the open water by becoming established as seedlings on the bottom, even though the water is in some regions quite shallow. It is likely that this is because of the very deep, light mud, in which it would be difficult for seedling establishment to take place and in which, once established, a young seedling would be easily choked by deposition of disturbed sediment or the growth of algae. Invasion of the loose mud occurs from the fringes, chiefly by *Scirpus validus* which, together with associated species, is responsible for a considerable accumulation of organic debris. This slowly compacts to build up a layer of peat towards the water surface. (Churchill (1961) records 310 cm of peat on one of the southern islands of the Loch.)

Once a compact bottom has been formed near to the water surface, conditions become favourable for the establishment of other species such as *Typha angustifolia* and *Machaerina juncea*, and the type of community included in Figure 6 is formed. This may be invaded by *Melaleuca*.



Figure 7.—The establishment of *Banksia littoralis* in a sedge meadow. The young *Banksia* plant is approximately 2 metres in height. The *Machaerina juncea* meadow is fringed by *Viminaria denudata* and *Lepidosperma gladiatum*.

TABLE 3

The distribution of cosmopolitan swamp and fen species and genera. Data for Eight-mile Creek Swamp (South Australia) from Eardley (1943), for Groenvlei (South Africa) from Martin (1960b), for European swamps in general from Tansley (1939) supplemented by Clapham et al. (1962), and for American swamps in general from Weaver and Clements (1938), Meunscher (1944), and Mason (1957). The comparison is based largely upon the tables given by Eardley (1943) and Martin (1960b), and includes some nomenclatural changes from Eichler (1965) and Blackall and Grieve (1965).

Western Australia (Loch McNess)	South Australia (Eight-mile Creek Swamp)	South Africa (Groenvlei)	Europe	North America
<i>Carex fascicularis</i> (formerly included in <i>C. pseudocyperus</i>) and <i>Carex appressa</i>	<i>Carex fascicularis</i>	other <i>Carex</i> species	other <i>Carex</i> species	<i>Carex pseudocyperus</i> and other <i>Carex</i> species
....	<i>Cladium procerum</i> (formerly included in <i>C. mariscus</i>)	<i>Cladium mariscus</i> var. <i>jamaicensis</i>	<i>Cladium mariscus</i>	<i>Cladium mariscoides</i> and <i>C. jamaicensis</i>
....	<i>Eleocharis acuta</i>	<i>Eleocharis palustris</i>	<i>Eleocharis palustris</i>
<i>Gahnia trifida</i>	<i>Gahnia trifida</i>
<i>Machaerina articulata</i> (= <i>Cladium articulatum</i>)	<i>Machaerina articulata</i>
<i>Machaerina juncea</i> (= <i>Cladium junceum</i>)	<i>Machaerina juncea</i>
<i>Scirpus nodosus</i>	<i>Scirpus nodosus</i> and <i>S. americanus</i>	<i>Scirpus americanus</i> (= <i>S. pungens</i>)	<i>Scirpus americanus</i>	<i>Scirpus americanus</i>
<i>Scirpus validus</i>	<i>Scirpus validus</i>	<i>Scirpus littoralis</i>	<i>Scirpus lacustris</i>	<i>Scirpus validus</i>
<i>Juncus pallidus</i> , <i>J. capitatus</i> , <i>J. bufonius</i> and <i>J. planifolius</i>	<i>Juncus pallidus</i> and <i>J. caespitosus</i>	<i>Juncus dregeanus</i>	other <i>Juncus</i> species	other <i>Juncus</i> species
<i>Lemna minor</i>	<i>Lemna minor</i>	<i>Lemna minor</i>	<i>Lemna minor</i>
<i>Triglochin procerum</i>	<i>Triglochin procerum</i>
<i>Triglochin striata</i>	<i>Triglochin striata</i>	<i>Triglochin striata</i>	<i>Triglochin striata</i>
....	<i>Phragmites communis</i>	<i>Phragmites communis</i>	<i>Phragmites communis</i>	<i>Phragmites communis</i>
<i>Typha angustifolia</i>	<i>Typha angustifolia</i>	<i>Typha angustifolia</i> and <i>T. capensis</i>	<i>Typha angustifolia</i> and <i>T. latifolia</i>	<i>Typha angustifolia</i> and <i>T. latifolia</i>
<i>Cotula coronopifolia</i>	<i>Cotula coronopifolia</i>	<i>Cotula coronopifolia</i>
<i>Senecio</i> aff. <i>luteus</i>	<i>Senecio</i> aff. <i>luteus</i>	<i>Senecio luteus</i> and <i>S. elegans</i>	<i>Senecio aquaticus</i>	other <i>Senecio</i> species
<i>Centella asiatica</i> (= <i>Hydrocotyle asiatica</i>)	<i>Hydrocotyle verticillata</i> (formerly included in <i>H. vulgaris</i>)	<i>Hydrocotyle verticillata</i>	<i>Hydrocotyle vulgaris</i>	<i>Hydrocotyle verticillata</i> and other <i>Hydrocotyle</i> species
<i>Epilobium billardierianum</i> (formerly included in <i>E. glabellum</i>)	<i>Epilobium billardierianum</i> and <i>E. pallidiflorum</i>	<i>Epilobium fluviatense</i> and <i>E. hirsutum</i>	<i>Epilobium hirsutum</i> and other <i>Epilobium</i> species	other <i>Epilobium</i> species
<i>Polygonum serrulatum</i>	<i>Polygonum serrulatum</i>	<i>Polygonum salicifolium</i>	<i>Polygonum lapathifolium</i> and <i>P. minus</i>	<i>Polygonum lapathifolium</i> and other <i>Polygonum</i> species

As the peat level continues to rise in the sedge vegetation, *Machaerina juncea* becomes dominant, and the fen formation is established. Invasion by dicotyledons such as *Viminaria*, *Phebalium* and *Banksia* then occurs. Transition to *Banksia* woodland as such, including the fringing *Xanthorrhoeas*, is presumably a very slow process, since this community occurs only on ground which is at a rather higher level than the fen. It is probable that the *Banksia* communities shown in Figure 2 have become established on areas which have never supported sedge communities, as well as in areas in which the peat has become sufficiently compact to support the accumulation of wind-blown sand and other debris. The fate of the *Melaleuca* community is equally uncertain, but it is possible that the accretion of soil may ultimately take place to such an extent as to make conditions unsuitable for the swamp paperbark, allowing the establishment of *Eucalyptus* woodland.

The position is further complicated by the possibility that the water level of the Loch may have been slowly rising, following a possible amelioration of climatic conditions after an arid period in Early-Recent times (Crocker 1959). Eardley (1943) has suggested that the Eight-mile Creek Swamp was slowly flooding because of increased rainfall in South Australia, and that the plant communities were showing a succession in which the swamp species were replacing woodland. An inverted succession of this kind may have occurred at Yanchep, but it must be remembered that a point has been reached at which the basin overflows. It is not known when the water level reached this point, but the occurrence of *Banksia* and *Melaleuca* seedlings in the swamp and fen communities suggests very strongly that succession is occurring in the direction open water to sedge community to woodland.

Another complication is afforded by the observation that within the large area of sedge communities there is a mosaic of different vegetation, and also marked irregularities in water depth. In some regions there are pools or what appear to be overgrown channels, while in other regions the change in topography is more subtle. One wonders if there may be changes of a cyclic nature in the communities, the *Machaerina* meadows being built up above the general level of the peat, but later collapsing or eroding back to allow the establishment of communities of deeper water. As mentioned above, the northern section of the Loch vegetation has been burned every three to four years since 1940, and no doubt by accident before that time. Irregularities in the severity of burning could establish important differences, not only in the species present in particular regions, but also in peat topography. A study of the ecological significance of fire in this region would be valuable.

Acknowledgments

We wish to thank Mr. H. E. Bancroft, Managing Secretary of the National Parks Board, for supplying information about Loch McNess; and Mr. G. G. Smith and other staff

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14.—A second large dumbbell-shaped australite, Ongerup, Western Australia, with notes on two other large australites

by George Baker

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Abstract

Following the discovery in 1960 of the largest known dumbbell-shaped australite at Cuballing, W.A., a second specimen of comparable size and shape has recently been found at Ongerup, W.A., approximately 110 miles distant and to the southeast of Cuballing. The Ongerup specimen, measuring 98.4 mm long, and weighing approximately 151 grams, is the second longest, and the eighth heaviest, australite recorded.

Straight, sinuous, and sometimes connected grooves (gutters) of U-shaped cross section and produced in a terrestrial soil environment by differential natural solution etching, dominate the sculpture of the exfoliated anterior surface and of the flaked equatorial zone, both of which are generally free from pits. Shorter, shallower etch grooves appear on parts of the non-spalled posterior surface which is otherwise generally smooth but has a dull lustre, a few small pits, and, like parts of the anterior surface, shows traces of the internal body schlieren that have been made evident by light terrestrial solution etching. Because of the effects of overall weathering and loss from the anterior surface by exfoliation of an aerothermal stress shell that was produced by aerodynamic heating during hypervelocity, one-way (earthwards) transit through the atmosphere, the specimen does not reveal any remnants of the type of sculpture attributable to aerodynamic processes.

Introduction

A large dumbbell-shaped australite from Ongerup is 1.6 mm shorter and about 25 grams lighter than the largest known dumbbell-shaped australite recently described from 110 miles to the northwest at Cuballing in Western Australia (see Fig.1); it has been made available for study through the courtesy of J. H. Lord, Director of the Geological Survey of Western Australia.

The specimen, which weighs about 151 grams and reveals well-developed natural solution etch grooves (gutters) but few pits, comes from a region of 72,500 square miles extent within which 71 per cent. of australites weighing over 100 grams have been found. This region occupies one twenty-eighth of the total area of the australite strewnfield. The australite was collected by Mr. K. A. O'Neill on his property some ten miles northwest of Ongerup in the southwest portion of Western Australia; it was recently presented to the Geological Survey of Western Australia by Mr. O'Neill. Ongerup is 210 miles southeast of Perth (see Fig.1) on approximately 34° S and 118° 30' E. The specimen was obtained from a soil environment when Mr. O'Neill, who was clearing his property of poison, revisited a spot where he had grubbed out the ground to ascertain whether the poison had been eradicated. He considered that he

should have seen the australite when he initially grubbed out the poison, but the chances are that the specimen was made visible after the grubbing process through washing away of masking soil by rain or winnowing by wind. Presumably the specimen came from up to 9 inches depth in the soil.

Size, weight, and specific gravity

Measuring 98.4 mm in length, the specimen from Ongerup is slightly shorter than the similar thick-waisted specimen, 100 mm long, from Cuballing, W.A. Its width ranges from 35.6 mm across the gibbosities to 33.2 mm across the waist region, while the depth (= thickness) measurements are 29.6 mm for the gibbosities and 26.8 mm for the waist region. These differences in dimensions are small but sufficient to enable classification of the specimen as a thick-waisted dumbbell-shaped australite (Fig.2).

The larger gibbosity is only 0.5 mm wider and 2.4 mm deeper than the smaller gibbosity, whereas in the Cuballing specimen, the dimensions of the two gibbosities are significantly different.

Its weight of 151.286 grams makes this specimen from Ongerup the second largest known dumbbell-shaped australite and the eighth heaviest australite so far recorded in the literature on australites. Including this specimen and (1) a specimen recently described from Newdegate, W.A. by McCall (1965), (2) two round australite cores from the Eastern Goldfield region and from Salmon Gums, W.A., (see Fig.1) recently brought to notice by W. H. Cleverly (on 31/10/66), and (3) four specimens from Victoria, now in the collection of the National Museum of Victoria, the total number of australites known to weigh over 100 grams each is increased to twenty-one (13 listed, Baker 1966 p.60). The total weight of these twenty-one large australites is 3,108 grams, which on a rough estimate would be about one hundredth of the total weight of all australites in known collections.

Prior to weighing in air and deionized water ($T_{H_2O} = 23^{\circ}C$) for determining its specific gravity, the Ongerup specimen was treated in 1:1 HCl in an ultrasonic vibrator to remove soil constituents and natural cementing substances that occurred within and attached to the walls and floors of some of the gutters. Its specific gravity value of 2.460, determined with a Walker's Steelyard, is significantly higher

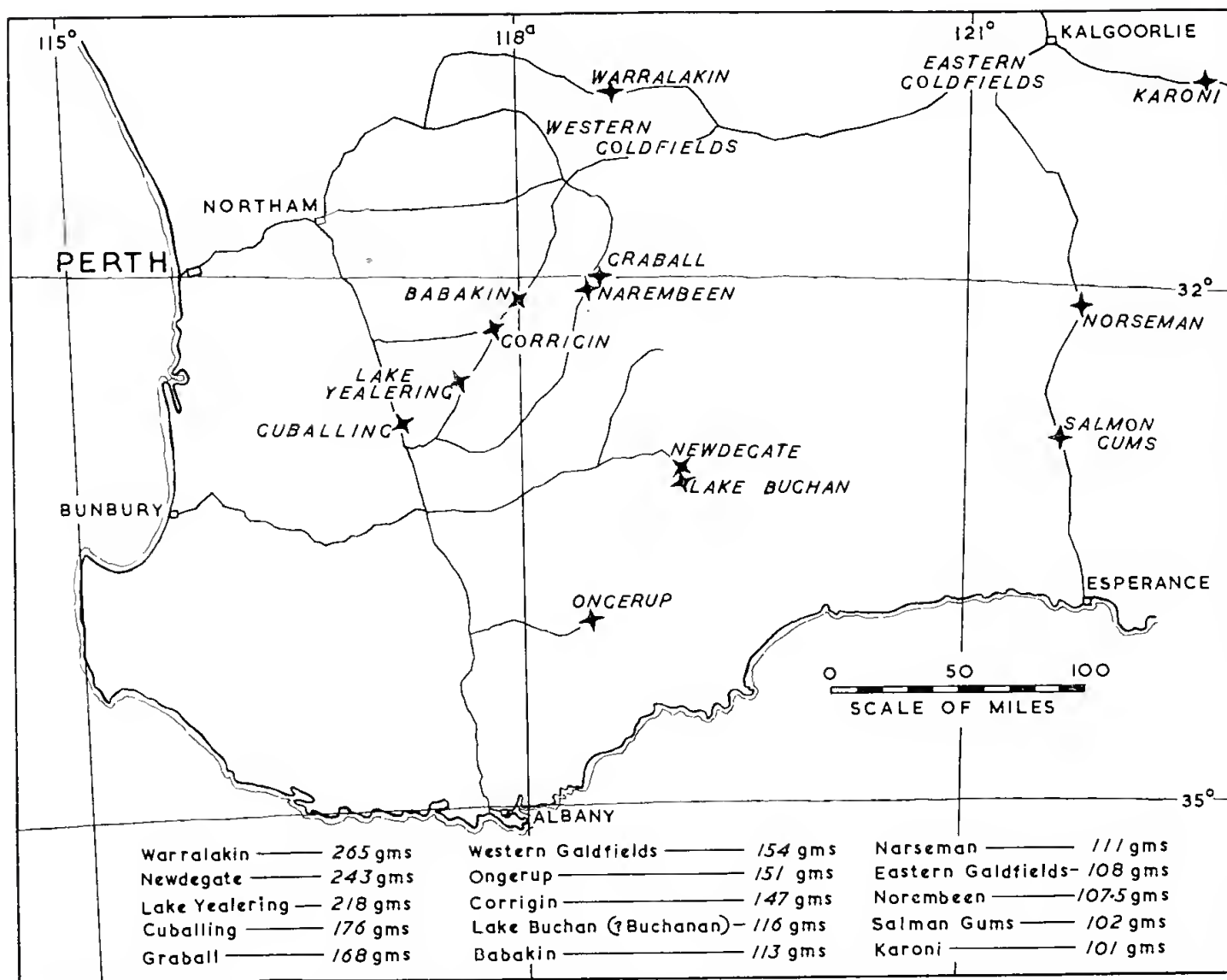


Fig. 1.—Sketch map of the southwest portion of Western Australia showing discovery sites of australites weighing over 100 grams. The sites for a specimen from the Western Goldfields area and one from the Eastern Goldfields region are not precisely known. Lines between localities represent roads.

than that for the Cuballing dumbbell-shaped australite (sp. gr. = 2.435). The difference is interpreted as a pointer to the Ongerup specimen being rather less acidic (some 2 to 2.5 per cent. less SiO_2) than the Cuballing specimen, provided that the difference in specific gravity is not a result of differences in gas bubble content, a check on which would mean destruction of the specimens for specific gravity determinations of the australite glass in the powdered state.

The average specific gravity value of the nine* only that have been determined among the twenty-one large australites recorded as having weights of over 100 grams each, is 2.431. Whereas the Western Australian large australites have an average specific gravity value of 2.437, the Victorian large specimens average 2.416, thus pointing to significant differences in composition for large specimens in the western and eastern portions of the australite strewnfield. Since silica content decreases with increase in specific gravity of tektite glass generally, it can be deduced from the specific

gravity-silica graph (see Baker 1959 p.56) that the large Victorian australites have a silica content of approximately 74 to 75 per cent., whereas the large Western Australian specimens contain approximately 72 per cent. SiO_2 .

Arcs and radii of curvature of the surfaces

Silhouette traces of the curved posterior and anterior surfaces at magnifications of just over $\times 4$ were prepared across the width of the slightly larger of the two gibbosities of the Ongerup dumbbell-shaped australite. The traces of the curvature of the two surfaces fitted reasonably well with the curvatures of circles constructed about them. The relationships of the arcs of curvature are shown by Fig. 2D, where the posterior surface is uppermost. The radii of curvature (R_B and R_F) were determined graphically as $R_F = 22.5$ mm, and $R_B = 16$ mm, where B and F refer to the posterior and anterior surfaces respectively. The radius of curvature (R_F) of the back surface of the Ongerup specimen is comparable with that ($R_B = 23.0$ mm) for the Cuballing specimen (Baker 1966), thus indicating that the primary forms from which

* Warralakin, Cuballing, Graball, Ongerup, Eastern Goldfields, Narembeen, and Salmon Gums in Western Australia; Port Campbell and Gymbowen in Victoria.

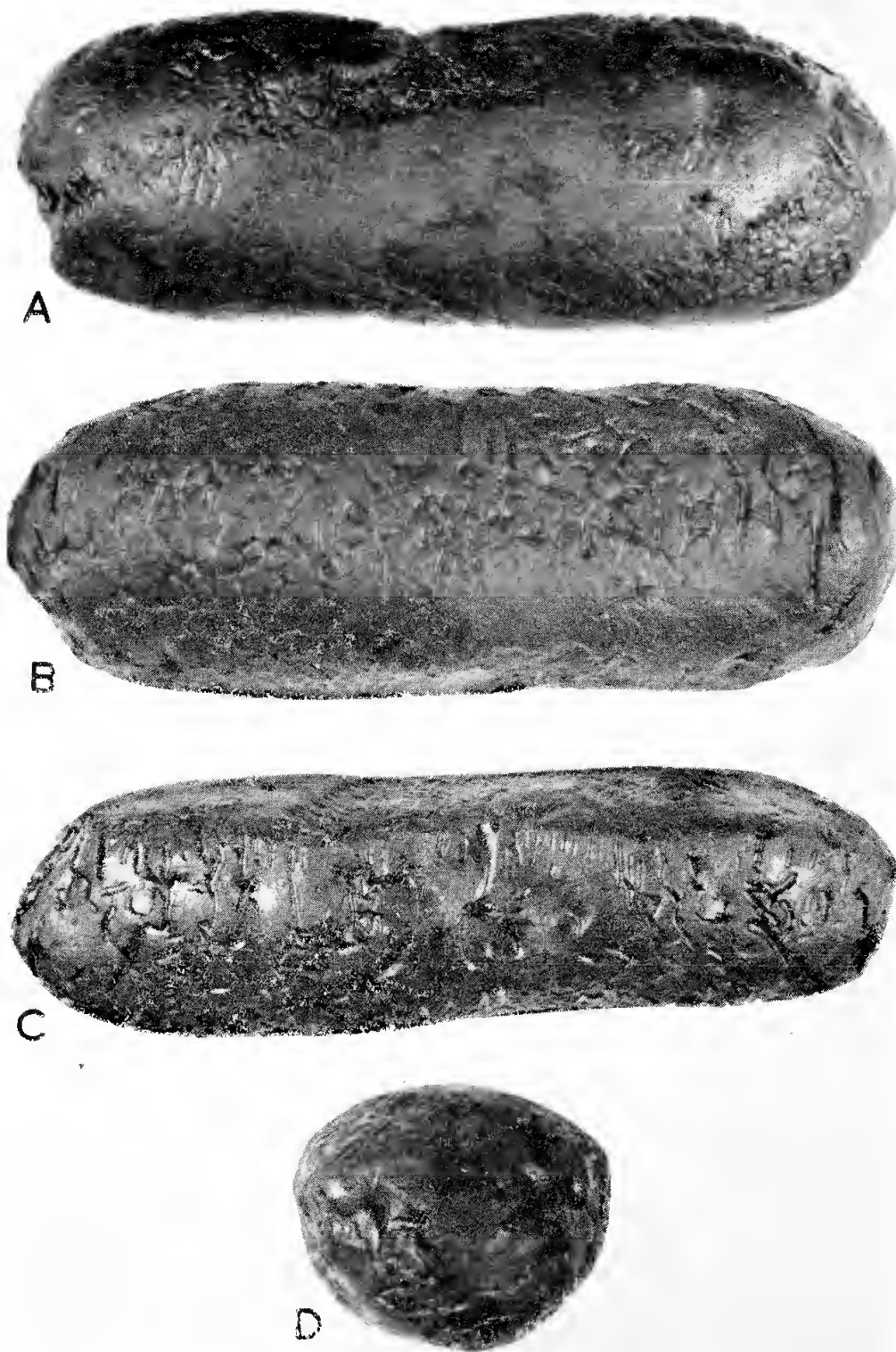


Figure 2.—Form and sculpture of the second largest known dumbbell-shaped australite, Ongerup, Western Australia. A.—Posterior surface showing generally smooth character with a few flow lines and rare, minute pits; short, shallow etch grooves occur on parts of the surface. B.—Anterior surface showing deeper and longer etch gutters transecting fine flow lines that trend generally parallel with the long axis of the specimen. C.—Side aspect (posterior surface uppermost) showing rim separating posterior and anterior surfaces, and etch gutters in the flaked equatorial zone comparable with those on the anterior surface. D.—End-on aspect of the slightly larger gibbosity (posterior surface uppermost) showing exfoliated anterior surface with occasional etch grooves. (A to C natural scale; D \times 1.05) (Photographs by G. J. Squance)

these two specimens were derived were evidently closely comparable in size. The radius of curvature (R_F) of the front surface, however, is significantly lower than that ($R_F = 20.0$ mm) for the Cuballing specimen, indicating that more glass was evidently lost from the forwardly directed surface of the Ongerup specimen as a consequence of (a) aerodynamic ablation during high speed atmospheric entry, followed by (b) differential exfoliation of the anterior surface causing shedding of the aerothermal stress shell after landing.

Sculpture of the surfaces

The dominant sculpture pattern is a consequence of natural solution etching in terrestrial soil, and the two surfaces, posterior and anterior respectively, show marked differences in the nature and extent of etching. (Figs 2A&B.)

In contrast with the pitted posterior surface of the Cuballing dumbbell-shaped australite (Baker 1966 Figs.1A&C), the posterior surface of the Ongerup specimen is much smoother, with a few schlieren made evident by small amounts of natural etching and occasional patches up to 1 mm below the general level of the tektite glass where short, shallow etch grooves have been developed (Fig.2A). The trends of the flow lines (schlieren) are fundamentally parallel with the long axis of the specimen.

The anterior surface shows a marked development of etch grooves (Figs.2B&C). In cross section, these are mostly U-shaped, less commonly rounded V-shaped, and are much more pronounced than on the Cuballing specimen (Baker 1966 Fig.1B).

The flaked equatorial zone (Fig.2C) is not particularly sharply marked because of modification by weathering after exfoliation, but it is nevertheless plainly distinguishable in places where the surface exposed by spalling has not been too extensively etch-grooved. The width of the flaked equatorial zone is up to 14 mm; numerous etch grooves cross this zone, sometimes extending across its width and continuing around on to the curving anterior surface (Figs.4&5); in the opposite direction, they generally terminate abruptly where the rim separates the posterior surface from the flaked equatorial zone (Figs.2C, 3A-C).

Another feature on the flaked equatorial zone, to which it is restricted, is represented by the flat, circular spalled areas from 3 mm to 4 mm in diameter (Figs.3A-C). These are evidently determined by the manner of spallation of the aerothermal stress shell. After etching, some of these appear horse-shoe shaped (Fig.3A), some become pitted (Fig.3C), others become concave (Fig.2C, left-hand end).

The gutters formed by etching are straight to branching, sometimes meandrine and vermicular in plan aspect (Figs.3,4&5). They vary up to

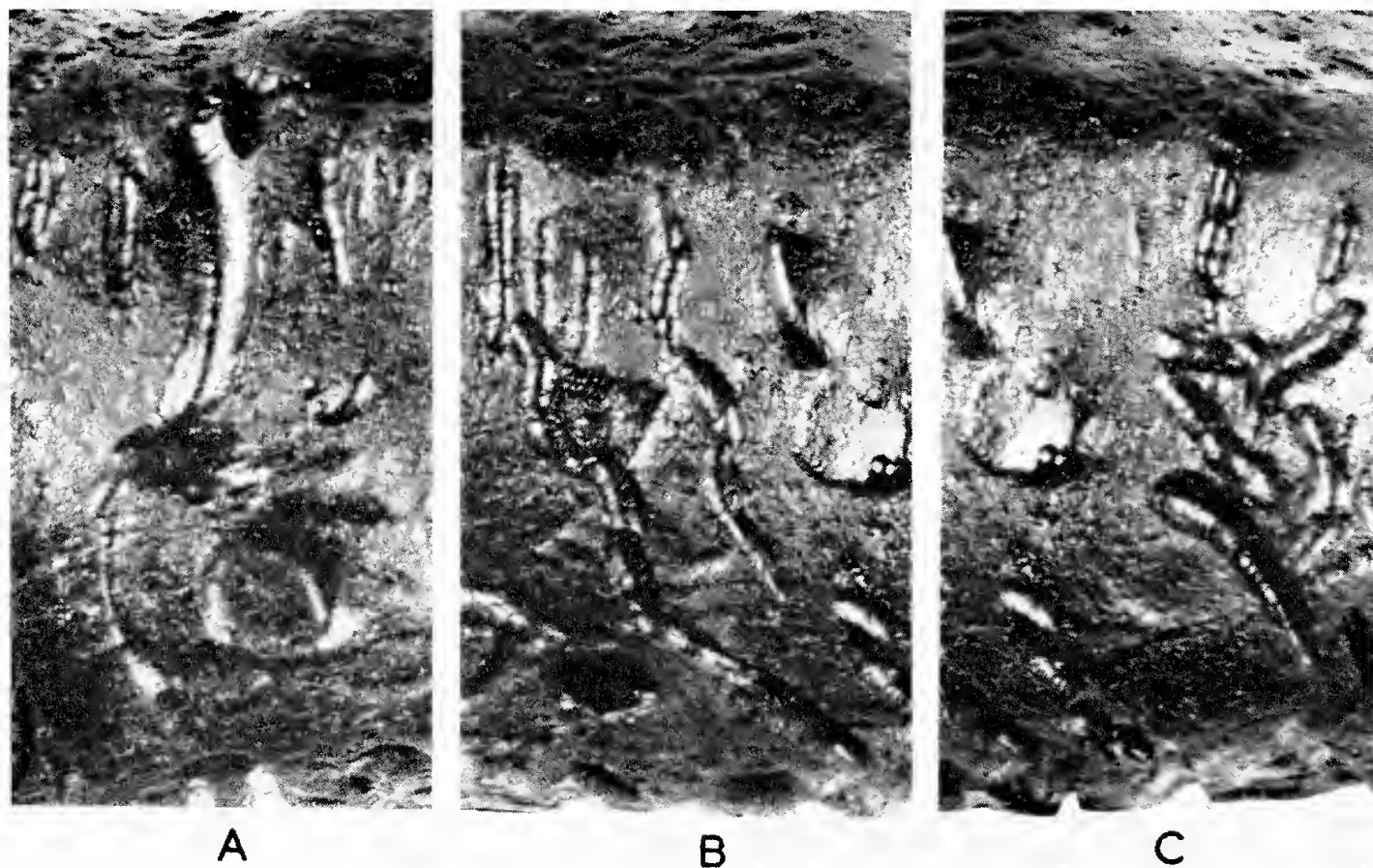


Fig. 3.—Etch gutters on the flaked equatorial zone, terminating at the edge (rim) of the posterior surface (uppermost in photographs), and occasional circular flat-bottomed spalled areas carrying an occasional etch pit. Dumbbell-shaped australite from Ongerup, Western Australia. A to C = $\times 3.9$. (Photographs by G. J. Squance.)



Figure 4.—Anterior surface showing etch grooves (gutters) with the sub-surface internal body schlieren exposed by etching on their walls and floors. Dumbbell-shaped australite from Ongerup, Western Australia. ($\times 4.1$) (Photograph by G. J. Squance)



Figure 5.—Anterior surface (continuation of right-hand side of Fig 4) showing sub-surface internal body schlieren (exposed on walls and floors of gutters) extending generally parallel with the long axis of the specimen. Dumbbell-shaped australite from Ongerup, Western Australia. ($\times 4.1$) (Photograph by G. J. Squance)

1.5 mm in width, up to 4 mm in depth, and up to 21 mm in length, but are never flat-bottomed because of their development on the curved surfaces of the australite glass. Sometimes the gutters are at slightly different levels relative to each other, indicating greater overdeepening by solution along some directions compared with others, and where such gutters intersect, those at the slightly higher level appear as miniature hanging valleys relative to those at the lower level (Fig.5—connected gutters in centre of photograph).

Characteristic features displayed on the walls and floors of a number of the etch gutters are cross striae (Figs.2C,3A-C,4&5) which represent the internal schlieren brought out by natural solution etching downward into the sub-surface regions of the flow-lined tektite glass. Sometimes the striae are more or less normal to the major trends of the gutters, but some are oblique to and less commonly parallel with these trends. This is a function of local variability in the trends of the internal schlieren relative to the major trends of the gutters, some of which trend across almost the entire width of the specimen and others trend obliquely to or almost parallel with its length (Figs.2B&5).

The dull lustre of parts of the australite glass on surface areas between the gutters is an outcome of micro-etch pitting (Figs. 4&5), possibly combined with the effects of a small degree of abrasional weathering. The more prominent types of etch pits encountered on some australites are generally insignificant in size and number on the Ongerup specimen. The few present are principally sub-circular to occasionally elliptical in outline, and up to just under 2mm across and about 0.5 mm deep; a few of these are visible towards the left central portion of the posterior surface (Fig.2A).

The prominent gutters on the Ongerup dumbbell-shaped australite are evidently not due directly to sculpturing by aerodynamic air flow, whether turbulent or otherwise. They occur on a surface which was part of the subsurface region of the interior of the specimen and hence was never exposed to aerodynamic forces. This surface has only been subsequently exposed by exfoliation and shedding of an original overlying aerothermal stress shell a few millimetres thick. Such grooves have not been obtained on the front surfaces of australites or other tektite glass models in experiments conducted to study ablational effects with aerodynamic flow instabilities at hypersonic velocities, but comparable grooves have been produced artificially by the chemical etching in 4% commercial HF of freshly fractured surfaces of tektite glass. Tektite glass typically breaks with a conchoidal to sub-conchoidal fracture and often reveals subsidiary ripple fracture marks crossing the conchoidal fracture surfaces. On etching the freshly fractured surfaces, pits develop in places in a few hours and grooves are produced along the trends of some of the ripple fracture marks. At a later stage in the etching process, the pits enlarge and their rims meet, while the shallow grooves pass into deeper and wider gutters. Inasmuch as the specimen came from a soil

environment, it is deduced that natural soil etchants were probably responsible for the development of the gutters during the period of several thousand years that the australite has lain in the moist soil environment. Available etchants in moist soils are the soil acids and alkalis, and the pattern of the etching sculpture may well be accredited to plant roots; parts of the pattern of distribution of the etch gutters certainly resemble that of groups of hyphal filaments of certain fungi (basidiomycetes) that grow in moist soils. The time factor is an unknown quantity relative to the operation and effects of soil etchants, likewise their potency, relative to tektite glass which is rather more durable than most other natural or artificial glasses. It is known from observations in the tektite strewnfields, however, that relatively deeply etched specimens generally come from areas where lateritization has been severe. Inasmuch as there has been extensive removal of silica from such lateritic horizons, it is not surprising that any associated tektite glasses undergo strong etching in such a milieu.

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Appendix

Two large, round australites, each weighing over 100 grams, were submitted by W. H. Cleverly for examination in connection with the recent discovery and recording of the larger types of australites from the south-west portion of Western Australia. These are registered as Nos. 9421 and 10,199 respectively in the collection of the School of Mines of Western Australia, Kalgoorlie.

No. 9421, a round core from 7 miles S.E. of Salmon Gums, W.A. (see Fig.1) is 44.6 mm to 46.4 mm in diameter (difference due to weathering) and 38.0 mm thick. It reveals a flaked equatorial zone averaging 18.5 mm in width, produced by exfoliation of the strained aerothermal stress shell that was secondarily formed on the forward surface during atmospheric flight earthward. Its weight is 102.37 grams, and the specific gravity as determined on a Walker's Steelyard is 2.45.

The principal sculptural features are a few meandrine gutters produced by etching in moist soils, occasional circular etch pits 1 mm across, and more numerous micro-etch pits that impart a fine "orange-peel" effect to parts of the sculpture pattern. A few sub-surface internal flow lines have been revealed by the effects of natural solution etching.

No. 10,199, a round core presumed to be from the Eastern Goldfields region, W.A. (see Fig.1), is 49.8 mm to 52.4 mm in diameter and 33 mm thick. The difference in the diameter measurements appears to be largely a consequence of

spallation and weathering. Its weight is 108.30 grams and the specific gravity as determined on a Walker's Steelyard is 2.44. Because of weathering, it is difficult to discriminate between the anterior and posterior surfaces, and there is no longer a clearly marked flaked equatorial zone. However, a very faint trace of a rim around parts of the periphery of the specimen helps to decide between the anterior and posterior surfaces respectively; the edge of the specimen is elsewhere rounded off by weathering. Only a few flow lines are faintly shown in places—these may have been more clearly defined at an earlier phase of natural solution etching, but are now nearly obliterated by the later effects of abrasional weathering. Few etch pits are present, probably for the same reason, but several etch gutters remain, although they

were most probably deeper before the onset of abrasion; one of these gutters is reverse S-shaped. The posterior surface has been artificially chipped on one side, revealing the highly vitreous lustre and conchoidal fracture of the tektite glass, with secondary ripple fracture marks detectible on the fresh, glassy fracture surface. The anterior surface reveals a flatter faceted area on one side, this probably being an effect of irregular spallation. The etch gutters on this surface are up to 2 mm wide, approximately 0.75 mm deep, and in places meandrine in plan aspect. Etch pits associated with them on the same surface are few in number, circular to elliptical in outline, and best revealed on the faceted portion of the anterior surface.

15.—Fossil bandicoots (Marsupialia, Peramelidae) from Mammoth Cave, Western Australia, and their climatic implications

by D. Merrilees*

Manuscript received 21 February 1967; accepted 18 July 1967

Abstract

It is shown that the bandicoot genera *Isoodon* and *Perameles* are represented in fossil deposits from Mammoth Cave, Western Australia, but not *Macrotis* or *Chaeropus*. The abundance of *Perameles* relative to *Isoodon* appears to have declined markedly between the time of accumulation of the Mammoth Cave fossil deposits and the present. Some environmental change must be postulated for this decline, and such change may be dated as late Pleistocene. It is possible, but not proven, that the environmental change may have been associated with an increase in rainfall.

Introduction

The occurrence of bandicoot remains among the fossils recovered early in this century from Mammoth Cave is reported by Woodward (1914); he lists *Thalacomys*, *Perameles* and *Isoodon*, but cites no specimens and provides no elaboration of his list. These three genera of bandicoots are listed by Bretnall, Chapman and Glauert (1926 p.70) again without elaboration. But later, Glauert (1948) lists *Macrotis* (= *Thalacomys*) and *Isoodon* but not *Perameles* from Mammoth Cave, still without elaboration. Later writers such as Lundelius (1960) have copied Glauert's 1948 list of bandicoots, and have made climatic inferences from the presence of *Macrotis* at Mammoth Cave (Cook 1960, Butler 1961). I have re-examined the bandicoot skull and mandible remains from Mammoth Cave and have compared them with modern specimens from the Western Australian Museum and other collections, cited below.

Modern bandicoots have been described by various writers, including Waterhouse (1846), Thomas (1888) Jones (1924) and Tate (1948). Numerous taxa have been proposed. I have followed Tate (1948) both in his nomenclature and in his taxonomic ranking of the bandicoots. It would appear that four genera of bandicoots have lived in the southern part of Western Australia within historic time, and should be considered as possibly occurring in the Mammoth Cave deposits; these four genera are *Perameles* Geoffroy 1803, *Isoodon* Desmarest 1817, *Macrotis* Reid 1837 and *Chaeropus* Ogilby 1838.

I have been able to examine one adult male skull and mandible of modern *Chaeropus* (Nat. Mus. Vict. C 470) and one juvenile (Aust. Mus. Syd. 422). To represent modern *Isoodon*, I have used only specimens of *I. obesulus* drawn from the well-watered south-western part of Western Australia. All Western Australian Museum specimens of modern *Perameles* and *Macrotis*, from whatever part of

Western Australia or the Nullarbor region, and of whatever taxon recorded, have been used as examples of their respective genera, and in addition, I have examined modern specimens of *P. nasuta*, *P. fasciata*, *P. gunni* and one of *P. eremiana* from the collection of the National Museum of Victoria. Various fossil samples have also been examined—see Table 2. Raw data on the modern and fossil specimens used, including their museum catalogue numbers, have been lodged in the library of the Western Australian Museum.

My criteria for distinguishing one genus of modern Western Australian bandicoots from another are set out in Table 1. Attention has been concentrated on structures likely to be preserved in fossil bandicoot remains; in practice, mandibular characters are most useful, especially that listed last in Table 1. Figure 1 shows the difference in relationship between the coronoid process and the horizontal ramus of the mandible in modern *Perameles* and *Isoodon*; I have seen only two specimens of *Perameles*

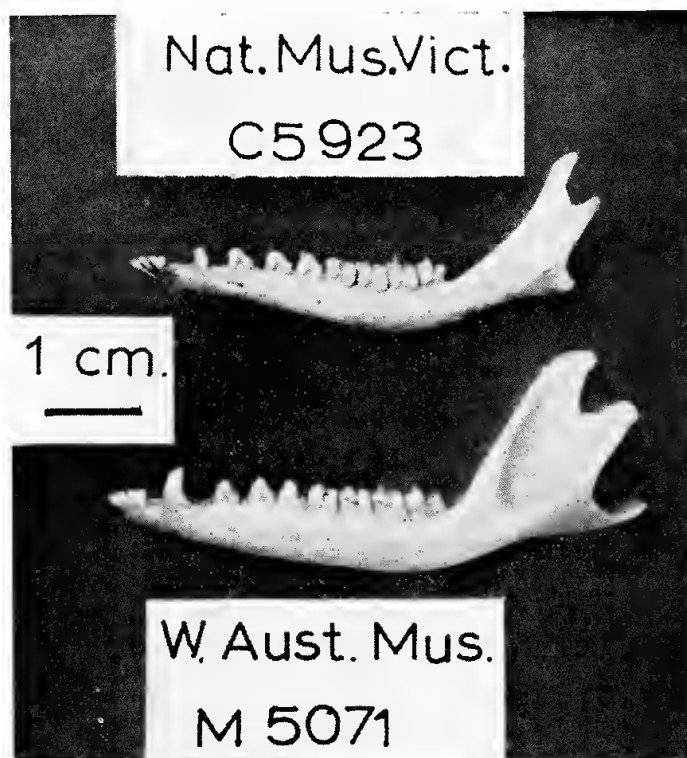


Figure 1.—Left mandibular rami, buccal view, of modern Victorian *Perameles fasciata* (above) and modern Western Australian *Isoodon obesulus* (below). Note smoothly curved junction of horizontal ramus with coronoid process in *Perameles*; contrast with obtuse angle in *Isocdon*.

* Western Australian Museum, Perth.

TABLE 1
Distinguishing features among genera of bandicoots living in Western Australia in historic time.

	<i>Macrotis</i>	<i>Isaachon</i>	<i>Peromyscus</i>	<i>Chaeropus</i>
Length relative to whole upper tooth row of $P_1 + P_2$ diastema	small	small	large	negligible
Size of C_1 relative to P_1 in horizontal section	large	often very large, but may be comparable	comparable	comparable
Shape of M^1 ; M^2 , M^3 in horizontal section	rounded blocks	rounded blocks	truncated triangles, tapering linguallly	truncated triangles, somewhat tapering linguallly
Shape of M^4 in horizontal section	length and width comparable	length and width comparable	length small, width great	length small, width great
Curvature in upper cheek tooth row	marked	slight (except <i>I. muerhausi</i>)	slight	slight
Bulla	anterior portion large, ovoid to pyriform, posterior portion also inflated	large, pyriform	large, hemispherical to hemi-ellipsoidal	small, pyriform to hemiellipsoidal
Muzzle shape	markedly contracting in front of M^1	gently tapering towards front	tapering towards front	markedly contracting in front of M^1
Mandibular ramus below tooth row	robust	robust	slender	robust
Size of C_1 relative to P_1 in horizontal section	comparable	often very large, but may be comparable	comparable, or C_1 smaller	comparable
Length M^1-M^4	exceeds 18 mm.	less than 16 mm.	less than 16 mm.	less than 16 mm.
Shape of M^2 in horizontal section	width usually exceeds length	length usually exceeds width	length usually exceeds width	length exceeds width
Posteroventral border of mandible, vertically below coronoid process	marked, but relatively small buccal process	buccal crest	buccal crest	very marked, relatively large, slightly hooked buccal process
Junction of coronoid process with horizontal ramus of mandible	obtuse angle	obtuse angle	continuous smooth curve	obtuse angle

TABLE 2

Range of variation in dimensions of tooth alveoli in fossil and modern bandicoots. In millimetres.

Sample	Individuals in mandibular sample	Length I ¹ -M ¹	Length M ¹ -M ²	Length x width M ¹	Diastema I ¹ -I ²	Width C ₁	Width P ₁	Length x width I ₃	Length x width I ₄	Length M ¹ -M ²	Length x width M ₂
<i>Perameles</i> — modern Victorian <i>P. fuscata</i>	2	35-36	11.6-11.9	1.8-1.9 x 3.0-3.3	1.9-2.4	0.6-0.9	0.7-0.8	2.7-3.2 x 0.7-0.9	2.7-3.0 x 1.1-1.4	12.6-12.7	3.1-3.2 x 2.3-2.4
<i>Perameles</i> — modern western <i>P. longicollis</i> group	11	31-35	9.3-11.1	1.3-1.9 x 2.8-3.3	1.0-2.1	0.5-0.9	0.6-1.0	2.7-3.2 x 0.7-1.0	2.5-3.1 x 1.0-1.4	11.1-12.1	2.6-3.1 x 1.8-2.2
<i>Perameles</i> — fossil, Mammoth Cave	12	0.9-1.5	0.7-1.2	3.0-3.8 x 0.9-1.2	2.6-3.5 x 1.0-1.5	12.3-13.9	2.9-3.6 x 1.3-2.3
<i>Perameles</i> — fossil, other caves in Augusta-Margaret River district	4	0.9-1.0	0.7-0.9	3.0-3.3 x 0.8-1.1	2.5-3.5 x 0.9-1.8	12.8-13.9	3.2-3.5 x 1.6-2.1
<i>Perameles</i> — fossil, caves in Nullarbor region	23	0.6-1.1	0.5-0.9	2.5-3.4 x 0.7-1.1	2.5-3.3 x 0.9-1.3	11.4-12.5	2.7-3.4 x 1.5-2.2
<i>Perameles</i> — fossil, caves c. 140 miles N of Perth	4	1.0	0.7-0.9	2.9-3.4 x 0.8-1.2	2.8-3.3 x 1.0-1.6	12.0-14.5	3.0-3.7 x 1.5-1.8
<i>Perameles</i> — modern Victorian <i>P. nasuta</i>	6	46-53	13.7-15.3	2.3-3.1 x 3.4-4.4	3.0-4.3	1.6-2.1	0.8-1.5	3.3-3.9 x 1.2-1.4	3.7-4.5 x 1.3-1.8	15.0-16.8	3.2-3.8 x 2.3-2.9
<i>Perameles</i> — modern Victorian <i>P. gunnii</i> , from one locality	6	41-44	13.5-13.8	1.8-2.2 x 3.1-3.6	2.0-2.9	1.0-1.2	0.6-0.8	2.8-3.3 x 0.8-1.3	3.3-3.8 x 1.1-1.5	14.8-15.5	3.5-3.8 x 2.5-2.6
<i>Isodon obesulus</i> — modern, south-western W.A.	30	34-42	11.7-13.8	2.5-3.7 x 2.9-4.2	0.5-1.2	1.0-2.8	0.9-1.7	2.6-3.4 x 1.0-1.7	2.4-3.5 x 1.3-2.2	13.6-15.9	2.5-4.1 x 2.6-3.4
<i>Isodon</i> — fossil, Mammoth Cave	5	...	11.3	2.4-2.6 x 3.2	...	1.5-2.0	0.9-1.4	2.4-3.7 x 1.0-1.8	2.3-3.5 x 1.3-1.7	13.2-14.8	2.9-3.7 x 1.7-2.9
<i>Macrotis</i> — modern W.A. (mainly <i>M. lagotis</i> , with one specimen ascribed to <i>M. sagitta</i>)	26	48-63	16.4-19.5	3.7-5.3 x 3.6-6.6	0.2-1.6	1.3-2.7	1.1-1.8	4.3-6.1 x 1.1-2.1	3.7-4.8 x 1.6-2.5	18.4-22.3	3.9-5.5 x 4.2-6.6
<i>Chaeropus</i> — modern Victorian	1	35	11.8	1.5 x 3.8	0.2	0.7	0.9	2.8 x 1.0	1.8 x 1.2	13.6	3.1 x 2.8
<i>Chaeropus</i> — fossil, Nullarbor region	22	...	10.5-11.6	1.6-1.9 x 2.6-3.1	...	0.8-1.1	0.6-0.9	2.8-3.6 x 0.5-1.0	2.1-2.7 x 0.8-1.5	12.0-13.4	2.7-3.4 x 1.9-2.6

(both large male *P. nasuta*) in which confusion with other bandicoot genera would be at all likely in this character.

Lundelius (1960) mentions the location (in the extreme south west of Western Australia) and age (late Pleistocene) of the Mammoth Cave fossiliferous deposits.

The Mammoth Cave fossil bandicoots

By the criteria of Table 1, two kinds of bandicoots may be recognized among the Mammoth Cave fossils, *Perameles* and *Isodon*. Specimens 66.2.178-193, 66.2.205-209, 66.3.101 and 66.7.12 (all mandibular fragments) represent *Perameles*. *Isodon* is represented by 63.7.132 and 66.2.202 (parts of skulls), and by 66.2.194-201, 66.2.203, 66.2.204, and 66.2.210-215 (mandibular fragments). I have found no bandicoot specimen in the Mammoth Cave fossil collection of the Western Australian Museum which I could identify as *Macrotis*.

It would appear unlikely that any confusion of *Perameles* with *Macrotis* could arise, but large fragmentary specimens of *Isodon* conceivably could be ascribed to *Macrotis*. Numerical data on *Perameles*, *Chaeropus*, *Macrotis* and *Isodon*, both fossil and modern, have been assembled in Tables 2 and 3. Since the teeth are frequently missing from fossil bandicoot specimens, alveolar dimensions rather than actual tooth dimensions have been recorded. Measurements are recorded only from those fossil and modern specimens in which $P^1_{1/4}$ and $M^1_{1/4}$ appeared to be fully erupted and in use.

Table 2 shows that there is overlap in range of variation in some dimensions between the Mammoth Cave *Isodon* sample and the modern *Macrotis* sample. In respect of width of alveoli of lower canines and of all three lower permanent premolars, the largest Mammoth Cave *Isodon* exceeds the smallest modern *Macrotis*. In all other eight dimensions which can be compared, modern *Macrotis* exceeds Mammoth Cave *Isodon*.

The modern sample of *Isodon* differs most markedly from modern *Macrotis* in molar and canine dimensions. *Isodon* may (but does not always) have conspicuously large canines, both upper and lower, far exceeding in relative and sometimes in absolute size, those of *Macrotis*. On the other hand, molar teeth in *Macrotis* usually greatly exceed those of *Isodon* in absolute size. Table 2 shows some overlap in range of variation in the molar dimensions recorded for modern *Isodon* and modern *Macrotis*, but the two genera are clearly separable on widths of the lower molars (exemplified by M_2 in Table 2) and by total length of the upper or lower molar rows. Table 2 shows that the fossil *Isodon* sample from Mammoth Cave also differs markedly from modern *Macrotis*, without overlap in range, in widths of lower molars and in total length of upper and lower molar rows. In addition, modern *Macrotis* exceeds Mammoth Cave *Isodon* in all other molar dimensions recorded in Table 2.

Only two individuals are represented by skulls in the Mammoth Cave fossil *Isodon* sample. One of these (63.7.132) retains suffi-

cient remnants of the bullae of both sides to show they conformed to the modern *Isodon* bullar characteristics. Both 63.7.132 and the smaller fragment 66.2.202 show the muzzle shape at about the P^1 - M^1 region, and it is not suddenly contracted in the manner characteristic of modern *Macrotis* and *Chaeropus*. Nor does the curvature of the molar row in 63.7.132 and 66.2.202 suggest *Macrotis* (or *Isodon macrourus*) rather than *Isodon obesulus*. Thus I am confident that no specimen from Mammoth Cave ascribed by me to *Isodon* should really have been ascribed to *Macrotis*. I am also confident that specimens of *Chaeropus* have not been confused with *Isodon*, because of the diagnostic differences set out in Table 1.

Individuals in the Mammoth Cave sample of *Perameles* tend to exceed those in the modern Western Australian sample in size, though there is overlap in range of variation for all those dimensions recorded in Table 2 except total length of the lower molar row; in this last dimension, the fossil sample from Mammoth Cave exceeds the modern *Perameles* sample absolutely, with means (see Table 3) differing significantly. It is possible, as Lundelius (1960) implies, that different species of *Perameles* are represented in these two samples.

Table 2 therefore lists other samples of *Perameles* drawn from the Western Australian Museum collection of fossil mammals. The age of these samples is not known, but all specimens except three appear to have been recovered from surface litter, not from excavations, in caves. Thus the specimens may be closer in average geological age to the modern specimens than to the Mammoth Cave fossil specimens recorded in Table 2. The Mammoth Cave fossils are not younger than 37,000 years B.P. (Lundelius 1960). Three samples of younger cave fossil specimens of *Perameles* are reported in Table 2, a small sample from caves not more than 20 miles from Mammoth Cave in the Augusta-Margaret River region, a small sample from caves about 140 miles north of Perth, and a larger sample from caves in the Nullarbor region.

If these younger cave fossil samples of *Perameles* be considered along with the modern western sample, and the whole composite sample compared with the older Mammoth Cave fossil sample, discrepancies between the younger and older samples still exist. Thus in width of C_1 , P_1 and M_2 , and length of P_3 some specimens of *Perameles* from Mammoth Cave exceed all other specimens available, though not greatly. In width of P_3 , length and width of P_4 , length of M_2 and length of M_1 - M_4 , range of variation in the combined younger samples of *Perameles* encompasses the range of variation shown by the older Mammoth Cave fossil sample. Neither the slight numerical discrepancies between these samples, nor any morphological considerations, demand that the Mammoth Cave specimens represent a different (larger) species of *Perameles* from the other specimens quoted. Table 2 also includes some samples of modern bandicoot species from eastern Australia. In those dimensions re-

corded in Table 2, there appear to be no closer resemblances between the Mammoth Cave fossil *Perameles* and modern eastern species than between Mammoth Cave fossil and modern western *Perameles*.

I have been able directly to compare cusp details in the fossil *Perameles* specimens with 15 modern specimens from Western Australia (ascribed to *P. myosura*, *P. eremiana* or *P. bougainvillei*) and with one specimen each of *P. fasciata* (Nat. Mus. Vict. C 5923 from the junction of the Murray and Darling Rivers) and *P. gunni* (Nat. Mus. Vict. C 1464 from Mt. Gellibrand, Victoria). In general, morphology of homologous teeth is very similar in all these modern specimens. However, neither Victorian specimen shows talonids as highly developed on P_1 or P_3 as do the modern Western Australian specimens, while C 1464 (*P. gunni*) differs from all the others in having a small cingular shelf on the antero-buccal aspect of M_1 . In C 1464, each of the lower molars has such a shelf, that on M_1 being smaller than that on M_2 , in turn smaller than that on M_3 , in its turn smaller than that on M_4 . C 5923 (*P. fasciata* from Victoria), M 2629 (*P. bougainvillei* from the Canning Stock Route, inland W.A.), and 10579 (*P. bougainvillei* from Dorre Island, W.A.) each shows a very small protruberance on the antero-buccal aspect of M_1 , the other modern western Australian specimens showing a continuous smooth wall in this region; but a marked shelf is evident on the antero-buccal aspect of M_2 in all these modern specimens, a much larger shelf on M_3 and a much larger shelf still on M_4 . C 1464 (*P. gunni*) differs from all the other modern specimens examined in exhibiting a smaller gradient of change in antero-buccal shelf size from M_1 to M_4 .

Thus insofar as my comparisons show, the modern Western Australian species (one or more) of *Perameles* differ from modern eastern *P. fasciata* and *P. gunni* in having more marked talonids on the lower permanent premolars. The modern Western Australian species resembles *P. fasciata* and differs from *P. gunni* in showing a progression in antero-buccal shelf size from nil or nearly nil on M_1 to a very marked structure on M_4 ; *P. gunni* shows such a shelf on M_1 , and progressively larger shelves on M_2 , M_3 and M_4 , but the gradient from before backwards is lower than in modern Western Australian species or in *P. fasciata*.

By these dental morphological criteria, available Western Australian fossil specimens agree with modern Western Australian species of *Perameles*. 27 fossil specimens of 29 showing some or all of P_1 , P_3 , M_1 and M_1 - M_4 gradient agree completely with the modern Western Australian species. The other two fossil specimens (66.3.22 from about 140 miles north of Perth, and 66.1.56 from the Nullarbor region) have rather small talonids on the first two permanent premolars, different in degree but not in kind from the modern specimens.

Taken in conjunction with the size characteristics set out in Tables 2 and 3, these minor considerations of dental morphology suggest

that neither the Mammoth Cave specimens of *Perameles*, nor any of the other Western Australian fossil *Perameles*, differ greatly from modern Western Australian *Perameles*. If one accepts the tentative suggestion of Tate (1948) that "the small bandicoots *P. bougainvillei*, (including *myosura*, D. M.), *fasciata*, *notina* and *eremiana* may be local races of a single widespread southern species . . .", then all the Western Australian fossil *Perameles* specimens cited above may be included in this species. Tate (1948) adopts the cautious concept of a "*Perameles bougainvillei* group" to cover his uncertain taxonomic situation, and I refer all the Western Australian fossil specimens cited above of *Perameles* to a "*P. bougainvillei* group" in Tate's meaning.

Climatic implications of the Mammoth Cave fossil bandicoots.

As noted above, inference of drier climatic conditions has been drawn from the supposed presence of *Macrotis* in the Mammoth Cave deposits. Since there is no *Macrotis* present, this climatic inference cannot now be entertained. In any case, the correlation of *Macrotis* with dry climate may not be very close. *M. lagotis* appears to be a very wide-ranging species. The Western Australian Museum collection includes modern specimens from Bridgetown, with a mean annual rainfall in excess of 30 inches, Cranbrook (over 20 inches) and other well-watered localities, as well as localities like Cue (less than 10 inches mean annual rainfall) which could be described as very dry. Species of *Macrotis* other than *lagotis*, however, would appear to be confined to very dry regions, according to the locality data supplied by Jones (1924).

If Tate (1948) is right in recognising *Isoodon obesulus* as a very wide-ranging species which includes the race *auratus*, then *Isoodon obesulus* can hardly be taken as an index of climate. The Western Australian Museum collection includes modern specimens of *Isoodon obesulus* (in Tate's sense) from Cowaramup (mean annual rainfall exceeding 40 inches) and from Lake Tobin (mean annual rainfall less than 10 inches, and very unreliable). The Cowaramup specimen (M 4522) demonstrates that *Isoodon* still survives in the neighbourhood of Mammoth Cave. The presence of *Isoodon* in the Mammoth Cave fossil deposit therefore carries no implication of a change in climate.

No specimen of *Chaeropus*, fossil or modern, from the vicinity of Mammoth Cave is known to me, though there is a record from the nearby Lake Cave of footprints, presumably modern, attributed to *Chaeropus castanotis* (E. A. Le Souef, 1905, reported in "The West Australian" 21st February, 1914.)

Perameles appears not to have lived in the Mammoth Cave region in historic time. There is no modern specimen of *Perameles* from the Cape Naturaliste-Cape Leeuwin region (extreme south-west of Western Australia) in the Western Australian Museum collection, and all the specimens in this collection suggest that the "*Perameles bougainvillei* group" represents rather dry, if not very dry, climatic conditions,

TABLE 3

Statistical summary of some alveolar dimensions in selected samples of fossil and modern bandicoot mandibles.

(Sex differences listed for *Macrotis* and *Isodon*, and difference in M_1 - M_4 length between modern western and Mammoth Cave fossil *Perameles*, are significant on student's *t* test.)

Sample	Dimension examined	No. of specimens	Observed range mm.	Mean mm.	Standard deviation mm.	Coefficient of variation
(From Western Australian Museum collections with exception noted below)						
<i>Macrotis lagotis</i> —modern, both sexes included, from many Western Australian localities	Width M_2	23	4.2-6.6	5.2	0.65	12.5
—same sample, males only	Length M_1 - M_4	13	19.5-22.3	21.1	0.92	4.4
—same sample, females only	Length M_1 - M_4	11	18.4-21.4	19.9	0.97	4.9
<i>Isodon obesulus</i> —modern, both sexes included, from South West Division of Western Australia	Width M_2	31	2.4-3.4	2.9	0.19	6.6
—same sample, known males only	Length M_1 - M_4	15	13.6-15.9	15.3	0.61	4.0
—same sample, known females only	Length M_1 - M_4	8	12.9-15.1	14.3	0.69	4.8
—same sample, known males only	Width C_1	15	1.6-2.8	2.2	0.34	15.6
—same sample, known females only	Width C_1	8	1.0-1.3	1.2	0.12	9.8
Mammoth Cave fossil <i>Isodon</i>	Length M_1 - M_4	4	13.5-14.8	14.2	0.61	4.2
	Width M_2	5	2.4-2.9	2.7	0.21	7.6
<i>Perameles bougainvillei</i> group—modern, both sexes included, from several widely separated Western Australian and Nullarbor localities	Length M_1 - M_4	11	11.1-12.1	11.7	0.36	3.1
	Width M_2	11	1.8-2.2	2.0	0.15	7.3
Mammoth Cave fossil <i>Perameles</i>	Length M_1 - M_4	10	12.7-13.5	13.2	0.26	2.0
	Width M_2	12	1.6-2.1	1.9	0.19	10.1
Other Augusta-Margaret River cave fossil <i>Perameles</i>	Length M_1 - M_4	4	12.8-13.9	13.3	0.46	3.4
	Width M_2	4	1.6-2.1	1.8	0.19	10.4
Nullarbor cave fossil <i>Perameles</i>	Length M_1 - M_4	22	11.4-12.5	12.0	0.32	2.7
	Width M_2	23	1.5-2.2	1.7	0.19	11.2
<i>Perameles gunni</i> —modern, National Museum of Victoria specimens, both sexes included, from Mt. Gallibrand, Vic.	Length M_1 - M_4	6	14.8-15.5	15.1	0.26	1.7
	Width M_2	6	2.3-2.6	2.5	0.04	1.6
Nullarbor cave fossil <i>Chaeropus</i>	Length M_1 - M_4	22	12.0-13.4	12.7	0.34	2.7
	Width M_2	22	1.9-2.6	2.2	0.21	9.4

though Glauert (1950) mentions a record of *Perameles* from the Albany region, most of which could be described as well-watered. The possibility should be considered that the presence of *Perameles* in the Mammoth Cave fossiliferous deposit indicates drier climatic conditions at the time of accumulation of this deposit than at present.

Not only was *Perameles* present at the time of accumulation of the Mammoth Cave deposit, but also it appears to have been the more abundant of the two kinds of bandicoots present. At least 13 individuals of *Perameles* are represented in the Mammoth Cave deposit as against 8 individuals of *Isoodon*. The Mammoth Cave deposits appears to me to have been a talus deposit, probably accumulating through holes in the cave roof. Thus it is probable that the animals represented in it fell involuntarily to their deaths. It is correspondingly improbable that the difference in representation of *Perameles* and *Isoodon* is due to *Perameles* being a cave-haunting and *Isoodon* a cave-avoiding form. Nor is it probable that *Perameles* suffered predation by a carnivore preferentially to *Isoodon*. The carnivores *Thylacinus*, *Sarcophilus*, *Thylacoleo* and even *Dasyurus*, which might have been bandicoot-eaters, have been reported from the Mammoth Cave deposit (Glauert 1948), but I know of nothing to suggest that the deposit was accumulated by these carnivores and that they were not the victims of falling through a hole in the cave roof equally with the other mammals represented in the deposit. It is simpler to postulate that the greater representation of *Perameles* than of *Isoodon* in the Mammoth Cave deposit reflects a larger population of *Perameles* than of *Isoodon* in the vicinity of the cave when the deposit was being accumulated. The deposit does not appear to be an owl pellet accumulation.

If *Perameles* (of the *bougainvillei* group) was once the commoner bandicoot in the Mammoth Cave region but does not now live there, whereas *Isoodon obesulus* was and still is present, it would appear reasonable to postulate some major environmental difference between the present time and the time of accumulation of the Mammoth Cave deposit. If the *Perameles bougainvillei* group represents drier climatic conditions, whereas *Isoodon obesulus* shows wide climatic tolerance, the major environmental change may well have been climatic; the climate may have been drier when the Mammoth Cave deposit was being accumulated than it is now. However, the ecological requirements of bandicoots appear not to have received extensive study, so that it would be rash to press this climatic supposition too far; other ecological factors than macro-climatic may have influenced the observed change.

Lundelius (1957) has shown from a study of superficial deposits in caves that *Perameles* has been more widely distributed in past, but not remote, time than at present. Elsewhere (Lundelius 1960) he has recorded *Perameles* at about 8,500 years B.P. and at about 12,000 years B.P. from shallow deposits in (an antechamber to) Nannup Cave, about 8 miles south of Mammoth Cave; *Isoodon* is also recorded from these same "Nannup Cave" deposits.

The Western Australian Museum collection of fossil mammals includes specimens from the Nannup Cave antechamber and from two other caves in the same (extreme south-western) region as Mammoth Cave, representing a total of 4 individuals of *Perameles*. Many more caves in this region have yielded many more individuals (at least 38) of *Isoodon*. As noted above, most of these specimens of *Isoodon* and at least one (66.2.53) of the few *Perameles* specimens in the Western Australian Museum fossil collection come from surface deposits within caves, whereas the Mammoth Cave specimens come from beneath a flowstone layer (Glauert 1910). These more superficial deposits presumably represent more recent times than the Mammoth Cave deposit.

Thus it would appear that the decline and ultimate extinction of *Perameles* in the Mammoth Cave region resulted from a slow trend rather than from a catastrophic change, and that this trend became evident at some time after the accumulation of the (buried) Mammoth Cave deposits but before the unknown but presumably relatively recent time of accumulation of most of the superficial south-western cave deposits. *Perameles* was abundant (relative to *Isoodon*) in the Mammoth Cave region over 37,000 years ago, was still present 8,500 years ago, and although in smaller proportion, was probably present still later, but not up to historic time. The environmental change which must be postulated to account for the relative decline in *Perameles* in the extreme south-west of Western Australia presumably therefore began in late Pleistocene time. This change may have been macro-climatic, and if so, is likely to have been one of increasing rainfall.

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Note added in press: G. E. Heinsohn (1966, *University of California Publications in Zoology* 80) reports ecological studies on *Perameles gunni* and *Isodon obesulus* in north western Tasmania. These species occur together, eat similar food (mainly earthworms and insect larvae) and in other ways are similar, but *Isodon* remains within a vegetation cover whereas *Perameles* forages in open areas. On this analogy, the late Quaternary increases in *Isodon obesulus* relative to *Perameles* cf.

bougainvillei in the Cape Naturaliste—Cape Leeuwin region, Western Australia may reflect an increasing density of low-growing vegetation or a reduction in open spaces. L. Freedman (1967, *Records of the Australian Museum* 27: 147-165) and L. Freedman and A. D. Jaffe (1967, *Records of the Australian Museum*, 27: 183-212) describe and illustrate skull and tooth characters in *Perameles*. Freedman (1967) cites "*P. gunnii*" and "*P. bouganville*" as the original spellings.

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